RESURGENCE POTENTIAL OF WATER HYACINTH (Eichhornia crassipes (MART.) SOLMS) IN LAKE VICTORIA

By

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Dedicated to my dear Dad, the late Yusito Masifwa, who inspired my search for wisdom right from my childhood.

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Water hyacinth, first reported on Lake Victoria in 1989, infested more than 80% of the lake coastline in less than a decade. The tropical climate, abundant nutrients, and absence of natural enemies to check its growth favored rapid proliferation. A control program for water hyacinth was initiated in Lake Victoria mainly using biological control, while herbicides were avoided due to environmental concerns. No effort was made to understand the role of environmental factors, especially nutrients, in promoting rapid proliferation. The overall objective of the study was to contribute information toward integrated management of water hyacinth, with particular attention given to understanding the role of nutrients in influencing hyacinth growth characteristics and proliferation on Lake Victoria.

Lake-based experiments, supplemented by laboratory nutrient bioassays, were undertaken to collect data on growth characteristics and biomass buildup under

varying nutrient concentrations. Assessment of phosphorus release from surface sediments collected from bays that experienced varying degrees of macrophyte infestation was addressed. Finally, phosphorus release from decomposing hyacinths under well oxygenated and hypoxic conditions was assessed.

Water hyacinth exhibited high growth rates and biomass accumulation under high nutrient concentrations. Growth was luxuriant at or above concentrations of 45 $\mu g\ L^{-1}$ SRP and 173 $\mu g\ L^{-1}$ NO_3-N; but less luxuriant at or below concentrations of 34 $\mu g\ L^{-1}$ SRP and 122 $\mu g\ L^{-1}$ NO_3-N. Crowding resulted in growth-form transformation from bulbous to non bulbous petioles, remarkably arrested vegetative propagation, and a switch from horizontal to vertical growth. No significant differences were found in carbon content and P release rates from sediments of different bays irrespective of magnitude of hyacinth infestation. Decomposing hyacinths released significantly more phosphorus under hypoxic than well-oxygenated conditions. Hyacinth decomposition altered water quality by depressing dissolved oxygen, creating acidic conditions, and elevating water column conductivity.

The major driving force behind growth characteristics of water hyacinth on Lake Victoria was nutrient availability. If not harvested, decomposition of water hyacinth biomass in the lake may significantly alter sediment characteristics and water quality. Sustainable management of water hyacinth must integrate environmental data, especially nutrients.

CHAPTER 1
GENERAL INTRODUCTION

Water Hyacinth Proliferation in Africa

Water hyacinth, Eichhornia crassipes (Mart) Solms, is an exotic, invasive, aquatic macrophyte native to Latin America. In its native range, it has natural enemies that control its prolific growth (Gopal 1987). Water hyacinth has now spread widely in the tropics and subtropics (Praphulla 1945; Penfound and Earle 1948; Pettet 1964; Boyd and Vickers 1971; Moorhead et al. 1988; DeBusk and Dierberg 1989) where it can have a variety of negative impacts (Gopal 1987), particularly on inshore fisheries. Colonization of large areas of tropical aquatic ecosystems by water hyacinth and other invasive aquatic plants such as Salvinia molesta (Mitchell) is of great concern in managing water resources (Mitchell 1974).

Earliest records on water hyacinth in Africa suggest that it was introduced in Egypt between 1879 and 1892 (Gopal 1987), in the Republic of South Africa about 1910 (Gopal 1987), and in the Democratic Republic of Congo between 1950 and 1951. By 1952, the plant was already on the Congo River. It was introduced in Sudan about 1958 (Gay and Berry 1959; Mohamed 1975; Obeid 1984) but was already in the Sudd region by 1956, and later spread to River Sobat. The rapid spread of water hyacinth in the White Nile was attributed to its high growth rate, the huge biomass that floated downstream, the high frequency of ships cruising the river, thunderstorms and squalls, and seasonal differences in the speed of downstream currents and wind direction (mainly southerlies during summer and northerlies in winter). It is probable that water hyacinth invasion in Sudan was via

tributaries of the Congo during high floods. Elsewhere in Africa, water hyacinth was introduced in Zimbabwe in 1937, Angola and Mozambique by 1942, Senegal by 1963 (Gopal 1987) and Tanzania in the early 1960s (Bailey and Denny 1978).

Water Hyacinth in Uganda

First reported on Lake Victoria in 1989 (Twongo *et al.*, 1991, Twongo 1993), water hyacinth is thought to have invaded Uganda waters initially in Lake Kyoga by 1988. This aquatic plant was probably in the lake before then. Next, it spread to the Upper and Lower Victoria Nile and Lake Albert. These water bodies have one thing in common; they are connected by the Nile River system. By 1994, water hyacinth covered almost the entire shores of the Upper and Lower Victoria Nile, and more than 60 % of the Lake Kyoga shoreline was already having the plants (Twongo 1993). By 1995, 80 % of the shores of Lake Victoria were infested (Twongo 1998). Water hyacinth continues to colonize other aquatic systems, particularly riverine ecosystems such as Ruwizi in western Uganda and some pools and brooks associated with the Manafwa River in the eastern part of the country.

Several environmental factors could have promoted the rapid proliferation of water hyacinth in Lake Victoria. The convoluted lakeshore (Beadle 1981) provided shelter from offshore winds, notably along the northern shore of the lake (Twongo 1996), thus helping stabilize weed mats that proliferated these bays. Agricultural development around Lake Victoria has resulted in deforestation, bush fires and drainage of swamps, leading to accelerated soil erosion (Hecky et al. 1996) and associated siltation of the littoral zone of the lake (Ogutu-Ohwayo et al. 1997). Siltation fouls breeding, nesting and nursery grounds of inshore fishes, particularly the Nile Tilapia, Oreochromis niloticus (Balirwa 1998), and contributes to nutrient loading of the lake via fertilizers applied on farmlands (Ogutu-Ohwayo and Hecky 1991; Bugenyi and Magumba, 1996). Urban and industrial

expansion along the lakeshore has increased sewage and other effluents discharged to the lake (Bugenyi & Magumba, 1996; Ogutu-Ohwayo et al. 1997), increasing nutrient loading and water pollution. Increased nutrient inputs from rain (Hecky *et al.*, 1996) and from industrial and domestic sewage and agricultural runoff have doubled the biological productivity (Oskam and Genderen 1996) of Lake Victoria during the last three decades (Hecky and Bugenyi 1992; Mugidde 1993). The rapid water hyacinth proliferation in Lake Victoria is also directly and indirectly affected by plant introduction via the Kagera River. The amount of water hyacinth that enters the lake through the Kagera River does not form a significant portion of the total plant biomass, since most of it is fragmented by the strong waves due to prevailing south westerlies. However, this biomass, once it is fragmented and sinks to the sediment surface, probably decomposes and releases enormous amounts of nutrients that further proliferation of water hyacinth in sheltered bays. This phenomenon is accentuated by eroded soils that flow into the Kagera River, giving it its brown color.

Given the extensive catchment area of Lake Victoria (184,000 km^2) and a flushing time of 140 years (Hecky and Bugenyi 1992), the retention capacity of nutrients is so high that eutrophication and anoxia may become long-term phenomena in the lake. An advanced stage of eutrophication under these conditions may be difficult to reverse (Jorgensen and Vollenweider 1988). The Great Lakes (in North America) provide an example of reviving a fishery and its associated water quality. In Lake Victoria, management measures have not addressed the role of nutrients in water hyacinth proliferation and other water quality issues; and yet nutrients are crucial for aquatic plant growth. Nitrogen and phosphorus are of particular interest, because primary productivity may be retarded by their scarcity (Beadle 1981). In Uganda, past control measures (mechanical/manual removal, chemical and

biological) did not address the role of nutrients in influencing the growth and proliferation of water hyacinth in the Lake Victoria basin.

An extensive literature base shows the potential of water hyacinth to exhibit rapid growth in nutrient-rich environments. For example, water hyacinth is used in wastewater treatment systems (Miner et al. 1971; Rogers and Davis 1972; Balakrishnan and Gunale 1979; Wolverton and McDonald 1979; Gupta, 1980; DeBusk et al. 1983; Reddy and Sutton, 1984; Aoyama et al. 1986; Sun et al. 1989; Mishra et al 1991; Aoyama and Nishizaki 1993; Aoi and Hayashi 1996; Mars et al. 1999) for its nutrient removal capability and biomass accumulation (Miner et al. 1971; Rogers and Davis 1972; Wolverton and McDonald 1975; Boyd and Scarsbrook 1975; Boyd 1976). The huge biomass of water hyacinth that occurred on Lake Victoria, particularly in sheltered bays such as Murchison, Waiya, Bunjako, and Thruston, could have been partly a result of nutrient enrichment. Patchy short term data exist on the nutrient status of some zones of Lake Victoria, but the relationship between nutrient status and water hyacinth growth has not been examined. By late 1998, biological control had remarkably negative impacts on growth conditions for water hyacinth; and loss of buoyancy resulted in large-scale sinking of water hyacinth biomass. This phenomenon was, however, unprecedented and occurred without data being collected on environmental influences (such as on fisheries and water quality). Effects of the sunken water hyacinth biomass on the ecosystem were not closely monitored, and thus are not fully understood. It can, however, be speculated that the sunken matter decomposed and released nutrients into the water column, and this could have altered ecosystem functioning spatially. Detailed data on growth of aquatic macrophytes in relation to nutrients are vital for developing lake management strategies.

Control of Water Hyacinth in Uganda

Proliferation of water hyacinth had major negative socio-economic attributes (e.g., disruption of fish-commodity system activities, navigation routes, water abstraction points, and hydropower generation at Nalubaale Dam). Water hyacinth fouled the sheltered littoral zones (Wanda et al. 2001) that are important areas for fish breeding, spawning and nurseries, especially for Nile tilapia (Balirwa 1998). These negative attributes increased the costs of social amenities.

Prompted by public outcry on negative socio-economic and ecological attributes of water hyacinth, the Government of Uganda, through the Ministry of Agriculture Animal Industry and Fisheries, co-ordinated water hyacinth control. Physical removal of weed biomass through mechanical harvesting at economically important strategic sites, in addition to manual removal at landing beaches and use of biological control agents (Neochetina bruchi and N. eichhorniae) in selected bays, were facilitated (NARO 2002). Chemical control, however, was deferred until after conducting an environmental impact assessment. By 1998, water hyacinth on Lake Victoria was controlled mostly through biological control. However, control of water hyacinth in riverine environments failed (NARO 2002), probably due to lack of establishment of biological control agents. With such remarkable success in controlling water hyacinth on the lake, there was laxity in control efforts, but scientists were suggesting potential resurgence of the plant because of favorable nutrient regimes, among other environmental factors.

Resurgence of Water Hyacinth in Lake Victoria

After the first phase of controlling the extensive plant mats on Lake Victoria up to 1998, the public noticed that hyacinth had started appearing as isolated clumps and solitary

plants by 2000; these plants could be the nucleus for further proliferation. A reconnaissance field survey confirmed resurgence of water hyacinth along the shorelines of most sheltered bays of northern Lake Victoria. In the open waters of the lake, however, drifting plant mats were common only in Murchison and Bunjako bays. By 2001, small clusters of water hyacinth reached the Nalubale hydropower dam via the Nile River.

Major centers of active resurgence, referred to as hot spots were identified as Murchison and Bunjako bays, in addition to Kirinya sewage outflow and the Kagera River. Some of these areas were characterized by high ambient N or P or both in the water column. Water hyacinths in these areas were characterized by rapid vegetative reproduction and high biomass build-up. Water hyacinths with bulbous leaves dominated the outer fringes of the stationary plant mats at the hot spots and were the major agents for vegetative propagation. The nonbulbous growth form was dominant behind the bulbous growth form in large plant mats.

Murchison Bay receives significant quantities of nutrients from Kampala via the Nakivubo Channel. Originally, the extensive papyrus swamp that surrounded Nakivubo Stream acted as an efficient buffer (Kansime et al. 1994) for the lake. Encroachment into the papyrus swamp has reduced the ability for this wetland to filter most of these pollutants. The problem has been aggravated by channelization and expansion of Nakivubo Channel, a project funded by World Bank, and has resulted in enhanced delivery of nutrients to the lake, leading to water hyacinth proliferation and permanent algal blooms. Reports from the Gabba Water Treatment Facility indicated increased color and odor of drinking water and frequent clogging of water filters due to high algal biomass, which have increased costs of water treatment and hence increased cost of drinking water.

In the Kagera River, like in other riverine environments, water hyacinth was not controlled. Large amounts of water hyacinth continue to drift downstream to the lake. However, this biomass does not contribute significantly to the viable plant biomass on the lake since most of it is fragmented by strong waves. Fragmented debris is strewn along the lakeshore or sinks to the sediment surface in open water, as evidenced by ponar grab samples and sediment coring experiments during this study. Thus, the major contribution of water hyacinth entering Lake Victoria via the Kagera River is via nutrient loading of fragmented plant material. Nutrient loading from this river is also likely to be significant via landscape erosion.

The Lake Victoria Environment

With an open water surface area of 68,800 km^2, Lake Victoria is the second largest freshwater body in the world and is shared by three countries: Kenya (6 %), Tanzania (51 %) and Uganda (43 %). The lake is characterized by diverse littoral habitats dominated by indigenous macrophytes of all growth forms (submersed, floating-leaved, free-floating, and emergent). The dominant free-floating plants are Pistia stratiotes, lemnids, Azolla sp. and others. The invasion of Lake Victoria by the exotic invasive water hyacinth by 1989 (Twongo et al. 1991) brought in new ecological dimensions, most of which are still unknown. Crul (1995) calculated the residence time at 138 years, which played a role in water hyacinth proliferation. The long retention time of the lake implies that external nutrient loading could lead to inlake levels that may sustain water hyacinth and other aquatic plants. Inundation of near-shore areas after lake level rise in 1960/1962 (Welcome 1965) and El-Nino rains of 1998 likely led to enormous release of nutrients to the lake from decaying organic matter.

The Research Problem

In Uganda, water hyacinths infested Lakes Kyoga and Victoria (Twongo et al. 1991; Taylor 1993) and threatened their economically important fisheries (Twongo and Balirwa 1996; Twongo 1996) and water quality (Bugenyi and Magumba 1996). The plant also became established along much of the shoreline of Lake Victoria (Twongo and Balirwa 1996). These infestations have now been brought under control by a combination of factors including biological control, but plant resurgence is still possible. Apart from warm conditions year round that promote rapid growth of water hyacinth (Gopal 1987), other environmental factors, in particular nutrients, may account for rapid proliferation (Howard and Harley 1998), especially in Lake Victoria. Although incompletely studied, clearly Lake Victoria is becoming eutrophic (Hecky and Bugenyi 1992; Lehman and Bronstrator 1993, 1994; Bugenyi and Magumba 1996; Hecky et al. 1996). Several parallel studies during the period of heavy infestation in Lake Victoria suggested the importance of shelter from offshore winds and shallow muddy bottom (Twongo et al. 1991; Wanda 1997; Balirwa 1998; Aketch 1999) as favoring water hyacinth establishment. Rapid proliferation of water hyacinth outpaced monitoring efforts in Lake Victoria and raised the question of what enhanced the rapid proliferation of water hyacinth in Lake Victoria. The problem of invasive aquatic plants in the Lake Victoria basin is likely to increase in response to the increasing human activities and accompanying impacts in the lake (e.g., pollution and soil erosion).

Water hyacinth is a relatively new feature in the Lake Victoria ecosystem. Widespread negative socio-economic aspects associated with water hyacinth infestation led to public

outcry, and the Government of Uganda responded by establishing, co-ordinating and facilitating control efforts. Control options put in place were as follows:

- **Mechanical harvesting.** This option was chosen at strategic economically important sites including the wagon ferry-terminal at Port Bell in Murchison Bay and the hydro-power generation facility in Jinja.
- **Manual removal.** This was encouraged at most fish-landing beaches. However, the magnitude of the problem was too large, and people lost interest in this approach.
- **Biological control.** This strategy proved viable; and likely contributed significantly to control of water hyacinth lakewide.
- **Use of chemicals** (herbicides) to control water hyacinth was avoided because of the herbicides' unknown impacts on the environment.

Thus it became evident that little attention was being paid to environmental factors controlling rapid proliferation of the plant in Lake Victoria and elsewhere in the Upper Nile region. Our goal was to diagnose the problem, rather than respond to crisis situations (end-of-pipe technology). The eutrophic state of Lake Victoria, whose literature base is rapidly expanding, could help explain the water hyacinth proliferation problem. Environmental managers and policy makers would benefit by using the accrued data to revive the health of the lake by putting in place mechanisms to mitigate further deterioration of the lake.

The major objective of this study was to assess the role of nutrients in water hyacinth growth and proliferation; and thus to assist water hyacinth management to increase sustainable fisheries and water quality in the littoral zone of Lake Victoria. To achieve this, the following specific objectives (with testable hypotheses) were identified

- Assess the accumulation and sequestering of nutrients and later production of organic matter by water hyacinth under different nutrient concentrations.
- Assess the role of water hyacinth-derived particulate organic matter on phosphorus release from surface sediments to the water column.
- Assess, under laboratory conditions, release of phosphorus from decomposing water hyacinths.

Based on the above objectives, three hypotheses were formulated:

- Nutrient (N and P) uptake and accumulation by water hyacinth leads to a proportionate increase in organic matter production and nutrient sequestering. Thus, there are particular sites in Lake Victoria where water hyacinth will proliferate on the basis of local nutrient variation.
- Presence of water hyacinth-derived particulate organic matter increases phosphorus release from surface sediments to the water column.
- Nutrient-release rates from decomposing water hyacinths are influenced by environmental factors, notably dissolved oxygen.

Study Approach

The study was designed to generate data/information on environmental factors (notably nutrients) that foster water hyacinth growth and proliferation. Water hyacinth became a characteristic feature in sheltered shallow bays with organic sediments, most of which were rich in nutrients. Thus research activities were mainly done in these areas in the Ugandan portion of the lake. The bays sampled were Berkeley, Macdonald, Hannington, Thruston, Murchison, and Bunjako (Figure 1-1). Their selection was based on previous observations of extensive water hyacinth cover during peak infestation. Fielding Bay was, however, occasionally (< 1 week) covered with mobile water hyacinth mats and was therefore used as the reference bay for the current studies. Logistical problems did not favor regular sampling of the Kagera River. Studies on growth were the randomized block design (RBD). For field growth experiments, the different sites were regarded as treatments while experimental enclosures were the blocks. For the semicontrolled laboratory growth experiments, the different levels of nutrients were the treatments while replicates for each treatment were the blocks.

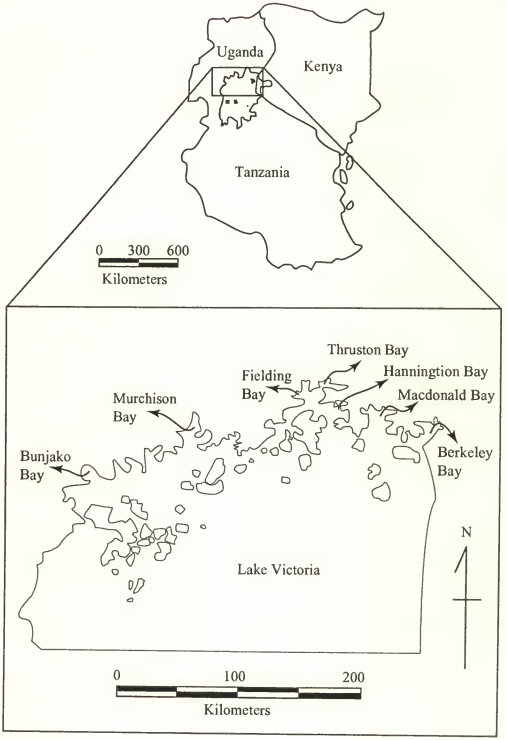


Figure 1-1. Map of East Africa showing location of Lake Victoria (above) and the Ugandan portion of the lake and bays sampled (below).

CHAPTER 2
ACCUMULATION OF NUTRIENTS AND PRODUCTION OF ORGANIC MATTER

Introduction

Despite widespread use of effective biological control agents and other measures, water hyacinth remains one of the aquatic plants that present most environmental problems globally, particularly in tropical and subtropical eutrophic waters (Heard and Winterton 2000). Water hyacinth has particularly high growth rates (Dunigan et al. 1976; Shiralipour et al. 1981) and can form dense mats under high nutrient concentrations (Sheffield 1967; Yount and Crossman 1970; Howard and Harley 1998). The favorable tropical climate and environmental factors promote massive growth of aquatic macrophytes including water hyacinth. In Lake Victoria, however, understanding of the relation among trophic state, water hyacinth proliferation, and the control process is lacking. An understanding of the ecology, plant-environment interactions, and distribution of plant biomass is increasingly needed for management of aquatic plants (Caffrey and Wade 1996). Environmental managers must anticipate (rather than react to) crises.

Our study examined the role of nutrients (notably N and P) and other environmental factors in influencing growth characteristics and nutrient accumulation by water hyacinth. Reddy and Sutton (1984) found that growth rates of water hyacinth are controlled by nutrient composition of the water, plant density, solar radiation, and temperature. In a related study, Reddy et al. (1989) observed that water hyacinth responds positively to

additions of nitrogen up to 5,500 $\mu g\ L^{-1}$; at higher concentrations, however, plant growth did not increase in the same degree. Reddy et al. (1990) evaluated net productivity and nutrient (N, P, and K) uptake and storage by water hyacinth at SRP concentrations of 60, 260, 560 1,060, and 2,560 $\mu g\ L^{-1}$ using 1,000 L outdoor tanks of 1.7 m^{-2}. They found that biomass yield increased with increased SRP up to 1,060 $\mu g\ L^{-1}$ but not at higher concentrations. Mansor (1996) found that high nutrient concentrations, notably soluble reactive phosphate concentrations greater than 100 $\mu g\ L^{-1}$, resulted in high productivity. Similar studies demonstrated luxury uptake of nutrients (N and P) by water hyacinth (Petrucio and Esteves 2000), but high concentrations of these nutrients reduced plant absorption and growth rates.

Absorptive capacity for nutrients by water hyacinth may also be influenced by N:P ratios in the water. Reddy and Tucker (1983) recorded best absorption rates of nitrogen and phosphorus by water hyacinth when N:P ratios were between 2.3 and 5; and this produced the highest water hyacinth biomass production. Earlier studies by Sato and Kondo (1981) found that greatest productivity occurred at an N:P ratio of 3.6 which was within the range established by Reddy and Tucker (1983).

Many plant species exhibit extension of root hairs in response to phosphorus deficiency (Foehse and Jungk 1983; Bates and Lynch 1996). For example, Ma et al. (2001) found root hair density of Arabidopsis thaliana to be highly regulated by phosphorus availability; density increased significantly in roots exposed to low phosphorus availability. This response may be an important strategy for enhanced phosphorus acquisition when phosphorus availability is low.

Water hyacinth grows vigorously (Balakrishnan and Gunale 1979; Wolverton and MacDonald 1979) and has a high nutrient content (Aoyama et al. 1986; Aoyama and

Nishizaki 1993). In tropical and subtropical systems, apart from algae, massive growth of floating mats of aquatic plants is often a severe problem (Njuguna 1993; Oskam and Genderen 1996), and water hyacinth is one of the species that caused most problems. The excessive development of algal and macrophyte biomass is a result of eutrophication, often attributed to human-induced nutrient enrichment of water with phosphorus and nitrogen (Oskam and Genderen 1996).

Studies of this sort have not received much attention in Africa as noted from limited available literature. For example, Desougi (1984) who studied mineral nutrient demands of water hyacinth in the White Nile, Sudan, used four treatments corresponding to 10 %, 50 %, 100 % and 200 % strength of Hoagland's solution. In a related study in the USA, DeBusk and Dierberg (1989) supplemented well water with nutrients at concentrations of 5,000 $\mu g\ L^{-1}$ NO_3-N and 1,100 $\mu g\ L^{-1}$ PO_4-P in addition to 4,500 $\mu g\ L^{-1}$ K, 3,600 $\mu g\ L^{-1}$ Ca, 600 $\mu g\ L^{-1}$ Mg, 800 $\mu g\ L^{-1}$ S, 500 $\mu g\ L^{-1}$ Fe, 200 $\mu g\ L^{-1}$ Mn, 200 $\mu g\ L^{-1}$ Zn, 10 $\mu g\ L^{-1}$ B, 10 $\mu g\ L^{-1}$ Cu, and 10 $\mu g\ L^{-1}$ Mo. They selected elemental concentrations of water in experimental tanks based on previous studies showing that nutrient concentrations and composition used were not limiting water hyacinth growth. Reddy and DeBusk (1984) did similar studies using concentrations of 10,500 $\mu g\ L^{-1}$ NO_3-N and 3,100 $\mu g\ L^{-1}$ SRP in addition to 10,500 $\mu g\ L^{-1}$ NH4-N, 23,000 $\mu g\ L^{-1}$ K, 20,000 $\mu g\ L^{-1}$ Ca, 5,000 μgL^{-1} Mg, 600 $\mu g\ L^{-1}$ Fe and micronutrients. Finally, Wahlquist (1972) assessed production of water hyacinth using N-P-K inorganic fertilizers at rates of 0-0-0, 0-8-0 and 8-8-0 to stimulate growth and found that plants in unfertilized tanks remained stunted.

In Lake Victoria, water hyacinth caused problems in sheltered, shallow bays dominated previously with native macrophytes such as Cyperus papyrus L. (papyrus) and

Vossia cuspidata (Roxb.) (hippo grass). Such bays also had organic sediments rich in nutrients. Bays of Lake Victoria (where water hyacinth proliferated most) included Inner Murchison and Bunjako (Namirembe/Katonga), and the Kagera River. Riverine systems are unique in that biological control failed to become established, and water hyacinth was not controlled (NARO 2002).

Several variables influence growth characteristics of water hyacinth, including plant density. For example, water hyacinth is heterophyllous and produces two distinct leaf forms (Watson et al. 1982; Center and Van 1989; Geber et al. 1992).

- Bulbous leaves have short expanded petioles of spongy chlorophyllous tissue with small leaf blades held close to or nearly parallel to the water surface. This growth form is characteristic of plants growing under low density such as in newly colonized sites or the outer fringes of stationary mats. Their vegetative propagation potential is usually high under favorable conditions, especially when nutrients are plentiful.
- Nonbulbous or canopy leaves are characterized by elongated (but not expanded) petioles, with large leaf blades that are almost perpendicular to the water surface. These dominate dense stands or shaded habitats, and their vegetative propagation potential is usually low.

Watson et al. (1982) noted that as plant density increased, water hyacinths gradually reverted to nonbulbous growth form.

Richards and Lee (1986) noted that water hyacinth displays marked foliar plasticity. For example, a single plant can produce short leaves with swollen petioles and long leaves with narrow petioles. Others (Penfound and Earle 1948; Richards 1981; Watson et al. 1982) reaffirmed the presence of different leaf types in a water hyacinth population at different locations. In addition, plants at the edge of a mat produce small leaves with expanded petioles, while those in the center of a mat produce long leaves with narrow petioles.

The major objective of this study was to assess the role of nitrogen and phosphorus in water hyacinth growth (biomass production and growth characteristics) in the littoral zones of Lake Victoria. To achieve this major objective, the following specific objectives were identified.

- Assess biomass production by water hyacinth under different concentrations of NO_3-N and SRP.
- Assess growth characteristics of water hyacinth under different concentrations of NO_3-N and SRP.
- Assess accumulation and sequestering of nitrogen and phosphorus by water hyacinth grown under different concentrations of NO_3-N and SRP.
- Assess phosphorus stocks (TP) in sediments and predict their potential influence on water hyacinth proliferation and growth characteristics if bioavailable.

Materials and Methods

Two approaches were used to collect data on ambient nutrient status and water hyacinth growth characteristics in the bays of Lake Victoria. First, broad scale surveys to collect data on nutrient status (N and P) in the water, and on growth characteristics of water hyacinth, were conducted once every 3 months in the bays of Berkeley, Macdonald, Hannington, Thruston, Fielding, Murchison, and Bunjako. Second, more detailed monthly data were collected on nutrient status and water hyacinth biomass build-up and growth characteristics. The latter approach was done in Thruston, Fielding, and Murchison bays; and later Bunjako Bay was included in monthly sampling schedules. These studies were supplemented by growth experiments conducted under semicontrolled laboratory conditions at the Fisheries Resources Research Institute (FIRRI) in Jinja, Uganda.

Field Surveys

Once every 3 months, field surveys were conducted in Berkeley, Macdonald, Hannington, Thruston, Fielding, Murchison, and Bunjako bays using a motorized canoe that enabled easy access to all sampling sites. Local communities participated in sample

collection to ensure that they would understand and appreciate the relevance of the studies being undertaken. Three sampling sites were established in each bay, other than Hannington Bay where there were 4 sites, with each site having three parallel transects 100 m apart. Along each transect, water samples were collected at 10 m, 60 m and 300 m from the shore to enhance statistical power.

During monthly surveys, three sites in each of Thruston, Fielding and Murchison bays, and two in Bunjako bays, were sampled (Table 2-1). At each site other than the

Table 2-1. Sites in bays sampled monthly

Thruston	Fielding	Murchison	Bunjako
Nkombe	Masese	Nakivubo channel	Katonga River inflow
Thruston Open	Wanyange	Bule	Bunjako
Kafunda	Kakira	Kisinsi	

open water sites of Thruston and Bunjako bays, there were three transects, 50 to 100 m apart with sampling locations at the shore and 60 m offshore. At the open water sites in Thruston and Bunjako Bays, sampling was done at three locations that were approximately 100 m apart. In the Nakivubo Channel, there were six transects, approximately 100 m apart, with three sampling locations per transect from the inflow towards the open water (a stretch of ≅ 600 m). The Nakivubo Channel had more transects (6 compared to 3 at other sites) due to being the major point-source nutrient inflow into Murchison Bay. Profiles of transects along which samples were taken, and/or experimental enclosures located are given in Figure 2-1. In addition, water of the Nakivubo Channel was distinct from lake water before it made confluence with the lake as was noted from its dark-stained waters, smell of raw sewage, low dissolved oxygen (usually < 1 mg L^{-1}), and high conductivity (> 250 μS cm^{-1}).

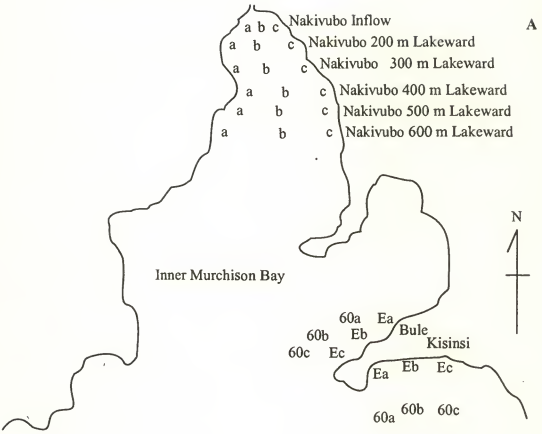


Figure 2-1. Map of selected bays of Lake Victoria showing transects where monthly data collection was done. Lower case letters (a, b, c) indicate transects a, b and c; upper case letter E represents the edge (i.e., close to the shore); the numeral 60 indicates 60 m lakeward from the shore, while 100, 200, 300, 400, 500, and 600 represent distance (in meters) from the inflow of a river/stream lakeward. A) Inner Murchison Bay. B) Thruston and Fielding bays. C) Bunjako Bay.

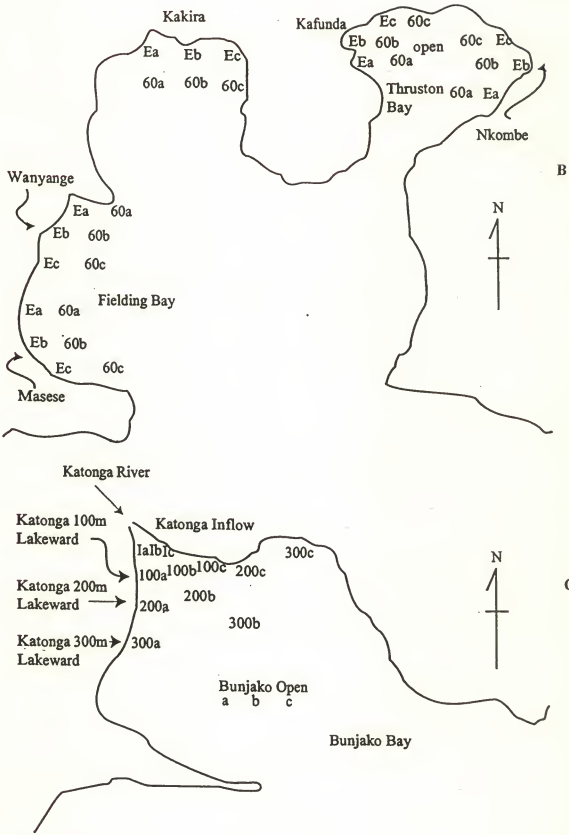


Figure 2-1. Continued

Water Chemistry

Physicochemical parameters (dissolved oxygen, conductivity, temperature, and pH) were measured insitu using Wissenschaftlich-Technische Werkstätten (WTW) dissolved oxygen (WTW Oxi 330), conductivity (WTW LF 330), and temperature-pH meters (WTW pH 197), respectively. Standardized measurements of physicochemical parameters were taken between 1100 h and 1400 h to minimize drastic influences of photosynthetic carbon fixation.

Water samples were collected using a 2 L horizontal Van Dorn sampler (Wildlife Supply Company, Michigan, USA). At sites deeper than 5 m, both subsurface and bottom water samples were collected. At sites less than 5 m deep, only subsurface samples were taken. It was assumed that at depths less than 5 m, the water column was homogeneously mixed. The water samples collected were immediately transferred to 0.25 L plastic bottles (BR15 Wagtech International, UK), placed on ice, and returned to the FIRRI laboratory for analysis of NO_3-N, TN, SRP, and TP. Before use, sample bottles were washed with 10 % $HCL_{(aq)}$ and rinsed three times with distilled-deionized water. This procedure minimized sample contamination. Analytical methods used are those described in the American Public Health Association (APHA 1988) (i.e., Cadmium reduction followed by Sulphanilamide and N-1-Napthylethylenediamine Dihydrochloride (NNED) for NO_3-N, persulfate digestion and Cadmium reduction for TN, ascorbic acid method for SRP, and persulphate digestion, and ascorbic acid method for TP).

Sediment Nutrients

Sediment cores were taken using a piston corer to which metal rings ($\cong$ 5 kg) were attached to provide the necessary weight to sink the corer into the sediment. Core tubes

were plexiglass (Rochester, New York, USA) (83 cm long x 6.7 cm internal diameter). The corer was equipped with a trigger, which, when operated, facilitated slicing of the sediment into the tube. The corer was then retrieved to just below the water surface, a tightly fitting rubber stopper plugged at the bottom of the tube to prevent loss of the sediment sample when leaving the lake. This procedure minimized disturbance at the sediment-water interface during sampling. Collected cores were allowed to stand for 2 h, and the overlying water was decanted slowly by pushing the rubber stopper at the bottom of each tube upwards using an aluminum rod (90 cm long) with a rubber head (3.4 cm diameter). The top of each sediment core was sliced into 1 cm sections down to a core depth of 5 cm and retained for analysis. Each core segment was put on a preweighed Pyrex Glass Petri Dish (Rochester, New York, USA). Sediment wet weight was determined using an electronic balance (to 0.01 g precision). Prior to drying at 55 °C, color and texture of the sediment were recorded, and then samples were dried in an oven until constant weight was attained. This procedure enabled determination of both water content and dry weight for each core segment.

Total Phosphorus (TP) Samples

Previously dried sediment samples were redried in the oven at 55 °C for 2 to 3 h to eliminate any moisture. A portion was removed from each sample and finely ground using an electric grinder. From each of the ground samples, 0.02 g was put in Destruction Bottles (100 mL). Ten mL of distilled-deionized water were added to the bottles, and the weight of each bottle determined without a lid. Samples, blanks (only distilled-deionized water) and standards (dilution series of stock TP solution) were then autoclaved at 1.5 atmospheres and 105 °C for 2 h and allowed to cool to room temperature. Original

weights (bottle + sample) were then restored by adding distilled-deionized water. One milliliter of each digested sample was transferred using a pipette (Gilson Pipetman, capacity of 100 µL to 1000 µL) to test tubes previously washed in 10 % $HCl_{(aq)}$ and rinsed three times with distilled-deionized water. Nine mL of distilled-deionized water were then added to give a final volume of 10 mL. To each test tube, 2 drops of 0.2 % para-nitrophenol were added followed by 90 µL of 4 M NaOH, giving a yellow color to the samples. One drop of 20 % H_2SO_4 was then added to change the samples to colorless. To each of the 10 ml of blanks, standards and digested samples, 2 ml of the mixed molybdate reagent was added. After 30 min, absorbance readings were determined using a Jenway 6300 Spectrophotometer at a wavelength of 885 nm, and sample concentration was calculated based on the regression analysis from the standard curves obtained.

Total Nitrogen (TN) Samples

This procedure is a modification of the Kjeldahl procedure used to determine TN in liquid or solid phase samples (Stainton et al. 1997) and utilizes salicylic acid and sodium thiosulphate. Thus, 0.10 g of sediment or plant samples were placed in the Kjeldahl tubes. To each, 6 mL of the mixture of Salicylic acid and Sulphuric acid (6.25 g and 250 mL, respectively) were added, followed by 0.5 g of sodium thiosulphate. The mixtures were then warmed for 10 min in a digester at 300 °C. After the tubes cooled to room temperature, a catalyst (15 g K_2SO_4 and 0.04 g $CuSO_4$) was added. The tubes were then returned to the digestion block and heated for 4 h until the samples became clear. They were then left to cool to room temperature before being removed from the digestion block. Three hundred mL of distilled-deionised water were then added to each sample prior to distillation using a Kjeldatherm-Vapodest 20. The distillates were collected in

Erlenmeyer flasks containing 40 mL of 4 % Boric acid indicator solution, then titrated using 0.1 N Hydrochloric acid. Concentration of TN was then calculated as in Eq. 2-1.

$$\% \text{ Total Nitrogen} = \frac{\text{Titer volume} * \text{Normality of HCl (0.1)} * 0.014 * 100}{\text{Sample weight (g)}} \quad \text{(Eq.2-1)}$$

where 0.014 = amount of N equivalent to 1mL 1 N HCl.. This was derived from the first principle:

$$\underset{1}{NH_{3\,(sol)}} + \underset{1}{HCl} \longrightarrow \underset{14\ g}{NH_4Cl.} \quad \text{(Eq. 2-2)}$$

The 1:1 ratio in Eq. 2-2 implies that 1 M HCl gives an equivalent 14 g of nitrogen per liter. This means, 1000 mL of 1 M HCl is equivalent to 14 g of N per liter.

Therefore, 1 mL of 1 M HCl ⟶ (14/1000) g of N in 1 mL = 0.014. This was then multiplied by 0.1 because the acid used was 0.1 N HCl instead of 1 M or 1N.

Water Hyacinth Biometrics Data

Nine water hyacinth plants, three from each transect in each bay, were collected by casting a quadrat (0.25 x 0.25 m^2) and randomly picking plants from each sampling site for determination of biometrics characteristics. Data were collected on lengths and widths of leaf blades, lengths of petioles and roots, growth form of the plants (bulbous or nonbulbous), reproductive potential (number of young offshoots per plant), and color of roots and leaves. Data on leaf dimensions were to help interpret growth condition in relation to environmental factors, especially nutrients (N and P), crowding and to some extent, herbivory by biocontrol agents.

Field (Lake) and Laboratory Growth Experiments

Water hyacinth growth characteristics

Growth experiments in the field were done using enclosures, and were supplemented by growth bioassay experiments to predict the influence of changing concentrations of N and P in surface waters on water hyacinth growth responses.

Experiments using enclosures made from a framework of loosely fitting horizontally arranged bamboo stems tied by nylon twines to facilitate free exchange of lake water were constructed in Thruston and Murchison bays to study the growth of water hyacinth under different ambient concentrations of N and P under field conditions. Bays of Thruston and Murchison were selected for these experiments because the former does not have any distinct point-source nutrient inflow, while the latter receives point-source nutrients via the Nakivubo Channel. A total of 18 enclosures were stationed in Thruston Bay, and 30 in Murchison Bay. The dimensions of each enclosure were 3 m long x 3 m wide x 1 m high (i.e., 9 m^3 rafts). Approximately half the height of each enclosure floated above the water surface to restrict water hyacinth movement, and the enclosures were positioned by anchoring with heavy stones (each stone was $\cong$ 10 kg), one at each of the four corners, using nylon twines. Each of the enclosures was stocked with five young bulbous water hyacinth plants lacking offshoots and stolons (herein referred to as a ramets which are single plants), and similar parameters as in Murchison Bay were monitored. The bulbous type was chosen due to its ability to float upright compared to the nonbulbous (canopy) growth form that tended to lie horizontal on the water surface. These enclosures were monitored biweekly for water hyacinth biomass changes and

biometrics data (numbers of ramets and leaves, wet mass, length of petioles and roots, and length and width of leaf blades).

In Murchison Bay, there were 6 enclosures each at Kisinsi and Bule (three placed close to the shore and three at approximately 60 to 100 m offshore) for purposes of replication. In Nakivubo Channel, however, due to its high point-source nutrient loading, 18 enclosures were placed along the flow gradient from the inflow to the open lake. At each transect perpendicular to the channel flow, there were three enclosures. In Thruston Bay, enclosures were set at Nkombe and Kafunda just like at Kisinsi and Bule. The open water site in Thruston Bay had three enclosures. At this site, enclosures were destroyed by waves periodically, so they were abandoned, but water quality data were always collected. All enclosures were anchored as in Murchison Bay. Assessment of changes in wet mass and biometrics data was expected to give information on growth characteristics and organic matter production in response to ambient nutrients.

The field experimental enclosures were each divided into 36 equal squares of 0.25 m^2 via a framework of nylon twine from which subsamples were collected. Non destructive sampling was used for plants from at least two small squares of each enclosure, and their mean number and wet mass were determined. The parameters were then used to extrapolate the number of plants and overall wet mass per enclosure using a factor of 36. This factor (36) was selected to account for 36 small squares in the entire enclosure that were derived as follows:

Each enclosure was 3 x 3 m^2 = 9 m^2; and each small square was 0.25 m^2.

Therefore, 9 m^2 ÷ 0.25 m^2 = 36 small squares per enclosure.

Three water hyacinth plants from enclosures were randomly selected by facing away from the enclosure and stretching the right arm to its maximum and picking only one plant from three different points. The picked plants were then used as subsamples for biometrics data and biomass (processing to ash free dry mass). Biometrics measurements (on leaf blade length and width, petiole length, and root length) were determined using a tape measure (to the nearest cm); these were later processed for biomass. The plants were divided into leaves, petioles, rhizomes and roots, and each category was finely chopped (< 1 cm^2) and wet mass determined using an electronic balance (precision to 0.01 g). Each sample was divided into two: one for biomass, and the other for tissue TN and TP determination. From each category, subsamples were put in preweighed glass Petri dishes and their wet mass determined.

- **Biomass samples.** These were dried in the oven (GALLENNKAMP Hotbox Oven Size 1) at 105 °C until constant weight was attained. This enabled determination of percent water content and dry mass. The dried samples were then put in porcelain crucibles and ashed in a furnace at 550 °C for determination of ash-free dry mass (AFDW). Estimate of AFDW from entire experimental enclosures was calculated backwards starting with AFDW from crucibles, dry mass in crucibles and estimated dry mass from wet mass of each experimental enclosure.
- **Nutrient samples.** Plant samples were dried in the oven at 55 °C until constant weight was attained, then allowed to cool to room temperature. Samples were then packed in polyethylene packets and stored in a dry place for subsequent processing. During preparation for tissue TN and TP analyses, the dried plant samples were re-dried in the oven at 55 °C for 2 to 3 h to eliminate any accumulated moisture. They were then processed for TN and TP as described above. The objective was to assess TN and TP contents in plant tissues and to relate them to available NO_3-N and SRP in the environment and their likely influence on biomass and growth of water hyacinth.

Growth Experiments under Semicontrolled conditions

Data from water hyacinths grown under semicontrolled conditions supplemented growth experiments undertaken in the field. Gerloff and Krombholz (1966) found that element concentrations in plant tissues are a reliable indicator of the availability of an

element in the environment in which a plant grew. I tested the hypothesis that N and P concentrations in water influence water hyacinth growth and tissue nutrient concentrations. Growth of water hyacinth was therefore monitored both in in situ enclosures on the lake and under semicontrolled laboratory conditions (bioassays).

A single bulbous water hyacinth plant was collected from a site free of biological control weevils, and cultured in tap water prior to the bioassay experiment to produce only uniclonal seed plants and hence eliminate genetic variability. The mother plant was multiplied until sufficient seed plants were attained, normally 3 months. During the period of multiplication, water in which the plants were growing was changed weekly to minimize accumulation of algae. Dead water hyacinth matter also was removed, and the tanks were washed to remove attached algae and other sedimenting matter.

An open-sided experimental shed (6 m long x 3 m wide x 3 m high) was constructed from local materials. The sides of the structure were screened to hinder contamination of the experimental set up from dust and insects. Lake water was collected at Naso Point in Napoleon Gulf near Jinja, an area assumed to have the least interference from human activities, especially nutrient loading. Water was collected in plastic tanks (50 L capacity, 41 cm top internal diameter, 37 cm internal bottom diameter, and 48 cm high) and brought to the experimental shed; these tanks were also used for growing water hyacinth. At the beginning of each experiment, the initial plant units consisted of parent ramets lacking stolons and daughter plants. Each tank was seeded with a single plant having bulbous leaves, and the tanks were randomly placed in the shed. The experiment was performed at three nutrient levels (high, medium, and low) (Table 2-2) in addition to a control, and care was taken to exclude all biological control weevils. Each level was in 3

replicates. The control tanks were filled with lake water, while the rest of the treatments were fertilized with varying amounts of the nutrient stock solution called "SUBSTRAL" (66 g L^{-1} inorganic nitrogen composed of 36 g L^{-1} NO_3-N and 30 g L^{-1} NH_4-N; and 30 g L^{-1} P_2O_5 and 67 g L^{-1} K_2O).

At the beginning of each experiment, plant wet mass, number of leaves, leaf blade length and width, and petiole and root length were determined. Plants were weighed after draining for 10 min followed by gentle wiping to remove excess water. Once weekly, the above parameters were recorded.

The first set of experiments was exploratory, and was terminated after 2 weeks due to dense algal growths on water hyacinth roots that resulted in death of plants in all treatments except the control. Data from this experiment were therefore considered

Table 2-2. Innocula per 50 L of lakewater

Nutrient level	Exploratory: µL of substral per 50 L of lakewater	First experiment: µL of substral per 50 L of lakewater	Second experiment: µL of substral per 50 L of lakewater
Control	000	000	000
Low-level innoculum	300	200	100
Medium-level innoculum	500	300	200
High-level innoculum	800	500	300

unreliable and not included in the final assessment. In subsequent trials, however, renewing water in experimental tanks twice weekly controlled algal growth. While first trial was exploratory, subsequent ones were aimed at adjusting nutrient concentrations to attain minimum concentrations of N and P for minimal water hyacinth growth. At the end of the experiment, subsample ramets from each set were separated into leaf blades, petioles, rhizomes and roots and treated as those from the lake-based experiments for

tissue TN and TP. A second set of samples was processed for biomass as described for lake-based experiments.

Growth rates of aquatic macrophytes are often expressed as specific growth rate (SGR) or as percent increase in biomass per day (Reddy and DeBusk 1984). Specific growth rates (Eq. 2-3) were also used to calculate the doubling time (Eq. 2-4) of water hyacinth populations. Specific growth rate (SGR) and doubling time were calculated as

$$SGR = \{(M_{tb} - M_{ta})/M_{ta}\}/\{t_b - t_a\} \quad \text{(Eq. 2-3)}$$

$$D_t = 0.693/SGR \quad \text{(Eq. 2-4)}$$

where SGR is the wet mass specific growth rate; M is wet mass; t_a and t_b are the times at which wet mass were measured (in days; $t_a < t_b$); Dt = doubling time (days).

Two plant properties are often used to measure and compare plant growth under varying nutrient supply: Relative Growth Rate (RGR) and the efficiency ratio. Mean values of RGR were calculated using Eq. 2-5. Thus

$$RGR = \{(M_t - M_0)/M_0\}/t \quad \text{(Eq. 2-5)}$$

where RGR is wet mass relative growth rate per day; M_t is wet mass at time t; M_o is initial mass at start of the experiment; t is time (days). Note that when calculating RGR, successive RGR are calculated with reference to the mass at onset of the experiment.

The Efficiency Ratio is the reciprocal of the internal nutrient concentration at the end of a time interval (Gerloff and Gabelman 1983), ans was calculated according to Eq. 2-6. Thus

$$\text{Efficiency Ratio} = 1/(\text{Tissue nutrient concentration}) \quad \text{(Eq. 2-6)}$$

The rate of increase of ramets was calculated using Eq. 2-7

$$RRI = \{(R_{tb} - R_{ta})/R_{ta}\}/\{t_b - t_a\} \quad \text{(Eq. 2-7)}$$

where RRI is the number specific growth rate per day; R_{ta} and R_{tb} is numbers of ramets (Numbers m^{-2}, $t_a < t_b$) between successive measurements; ta and tb = time interval (days).

One-Way ANOVA was used to determine significant differences in physicochemical parameters (dissolved oxygen, temperature, pH, conductivity and nutrients) through multiple comparisons of means for data collected from the lake due to

the randomized mode of data collection. For data from semicontrolled water hyacinth growth experiments, Repeated Measures Test was used to determine differences. Pearson's correlation coefficient was used to predict the influence of NO_3-N and SRP concentrations on water hyacinth biometrics data, while regression between nutrients and growth was used to predict growth.

Results

Lake Victoria Physicochemical Parameters

Average values of physicochemical data from surface waters sampled once every 3 months between April 2001 and August 2002 are given in Figure 2-2. The cumulative numbers of measurements taken for each parameter between May 2001 and August 2002 were 6 from Sio River inflow, 30 from Berkeley Bay, 64 from Macdonald Bay, 93 from Hannington Bay, 34 from Thruston Bay, 52 from Fielding Bay, 70 from Nakivubo Channel, 63 from Inner Murchison Bay away from Nakivubo Channel, 72 from Katonga River inflow, 21 from Bunjako Bay and 9 from the Kagera River. Due to logistical problems, some sampling periods were missed out and this resulted in different sample sizes.

Low dissolved oxygen (D.O.) concentration characterized inflow of the Katonga River, the Nakivubo Channel and Sio River (range 1.2 to 4.1 mg L^{-1}). The rest of the sites had average D.O. concentrations above 5 mg L^{-1} (Figure 2-2 A). The very low dissolved oxygen at the Katonga River inflow was probably due to its waters passing through an extensive papyrus swamp where most of the oxygen, though not assessed, was likely taken up through various biogeochemical processes. In the Nakivubo Channel, however, low D.O. was attributed to organic and inorganic loading arising from upstream reaches in Kampala; values < 1 mg L^{-1} were quite common in this channel.

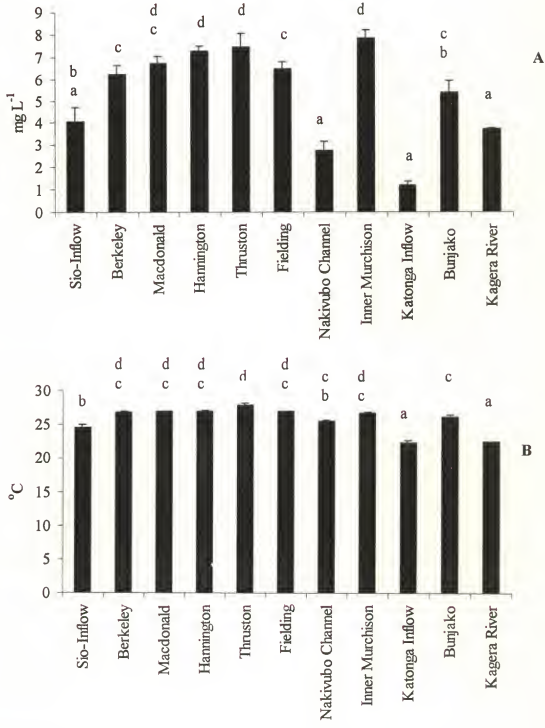


Figure 2-2. Surface water limnological data from selected bays of Lake Victoria from May 2001 to August 2002, measured between 1100 and 1400 h. A) Dissolved oxygen (mg L^{-1}). B) Temperature (°C). C) pH. D) Conductivity (µS cm^{-1}). Letters above graphs indicate groups that were not significantly different ($P > 0.05$)

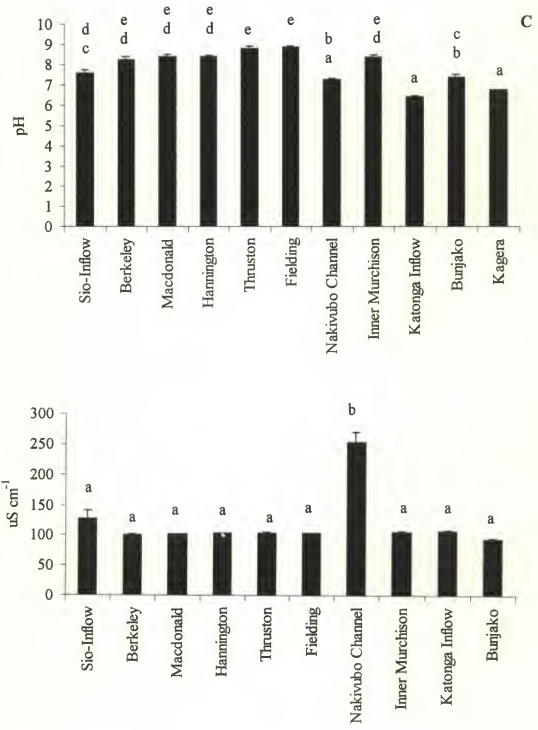


Figure 2-2. Continued.

Temperature (Figure 2-2 B) varied minimally during the sampling period at all sites. Rivers had lower mean temperatures (range 22.3 to 25.5 °C) compared to bays

(range 26.1 to 27.9 °C). Among rivers, the Katonga River inflow (22.3 ± 0.2 °C) and the Kagera River (22.4 ± 0.1 °C) had the lowest mean temperatures compared to the Nakivubo Channel (25.5 ± 1.2 °C). Slightly acidic to circumneutral conditions were associated with rivers and streams (pH range of 6.4 to 7.2). Other sites had pH range of 7.3 to 8.8 (Figure 2-2 C). Conductivity (Figure 2-2 D) was highest in the Nakivubo Channel (Mean 254 ± 16 $\mu S\ cm^{-1}$) associated with inorganic loading from Kampala. Other site had mean conductivity in the range 94 to 127 $\mu S\ cm^{-1}$. No data are available for the Kagera River due to breakdown of the conductivity probe.

Apart from the open water site of Thruston Bay (> 5 m deep), all sites sampled were in the depth range between 0.4 ± 0.1 m at the Sio River inflow and 3.6 ± 0.5 m in Fielding Bay. The shallow nature of these sites did not necessitate taking data along a depth profile.

Data on nutrient (N and P) concentrations of surface water in selected bays of Lake Victoria are given in Figure 2-3. Significantly higher concentrations ($P > 0.05$) of NO_3-N were associated with inflows of the Sio and the Kagera rivers (range 62.3 to 79.7 $\mu g\ L^{-1}$). The higher concentration of NO_3-N in the Sio River was a localized phenomenon at the inflow and did not extend 100 m from the inflow into the open waters of the lake. Mean concentration of nitrates at the Katonga River inflow, and at other sites other than the Sio and the Kagera rivers, were not significantly different ($P > 0.05$) (range 10.1 to 24.3 $\mu g\ L^{-1}$).

Soluble reactive phosphorus (Figure 2-3) was significantly higher ($P < 0.05$) in the Nakivubo Channel (range 228.1 to 252.1 $\mu g\ L^{-1}$), while average concentrations at the Sio and the Katonga river inflows (range 42.6 to 91.0 $\mu g\ L^{-1}$) were not significantly different

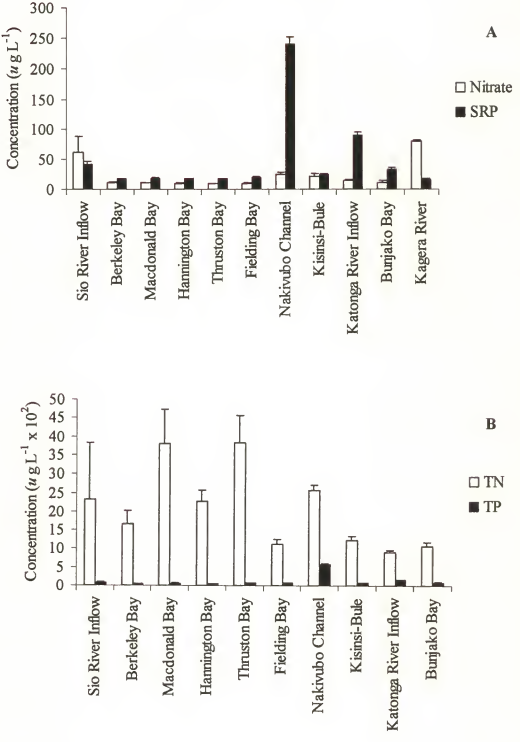


Figure 2-3. Nitrogen and Phsphorus concentrations in surface water from selected bays of Lake Victoria. A) NO_3-N and SRP. B) TN and TP.

($P > 0.05$) from each other, but were significantly lower ($P < 0.05$) than in the Nakivubo Channel. Concentrations of SRP at other stations (range 17.1 to 33.7 $\mu g\ L^{-1}$) were not significantly different ($P > 0.05$) but were lower than in both the Nakivubo Channel and river inflows.

At all sampling sites, there were no significant differences ($P > 0.05$) in concentrations of total nitrogen (TN) (range 896.1 to 3833.4 $\mu g\ L^{-1}$, Figure 2-3 B). Significantly higher ($P < 0.05$) mean concentrations of TP were recorded in the Nakivubo Channel (531.2 to 599.0 $\mu g\ L^{-1}$), while there were no intersite significant differences ($P > 0.05$) in mean TP concentrations at other sites (range 51.4 to 157.3 $\mu g\ L^{-1}$).

At sites where water hyacinth growth was rich (e.g., the Nakivubo Channel), ambient SRP concentrations were high and were inversely related to dissolved oxygen

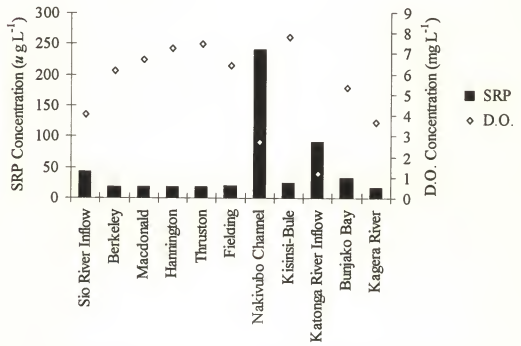


Figure 2-4. Relationship between SRP and D.O. in selected bays of Lake Victoria.

(Figure 2-4), with a negative significant correlation (at $P = 0.05$, $r = -0.625$). Significantly lower ($P < 0.05$) SRP concentrations could have been a result of increase in dissolved oxygen with distance into the open lake that could have led to binding of P to oxidized cations such as Fe and Al (Togwell and Schindler 1975; Lovely 1991; Friese et al. 1998). For example, a significant positive ($P = 0.01$) correlation was found between dissolved oxygen and distance in the Nakivubo Channel ($r = 0.913$), and in the Katonga River ($r = 0.933$). In addition, SRP concentration decreased along the flow gradient of the Katonga River and the Nakivubo Channel, with significant ($P = 0.01$) negative correlations ($r = -0.998$ for the Katonga River, and $r = -0.991$ for the Nakivubo Channel).

Water Hyacinth Biometrics Data from Selected Bays of Lake Victoria

The cumulative number of measurements (across sites and times) were 51 for Berkeley, 52 for both Macdonald and Hannington, 88 for Thruston, 67 for Fielding, 219 for Nakivubo Channel, 117 for Inner Murchison, and 93 for Bunjako. Luxuriant water hyacinths were found in the Nakivubo Channel of Inner Murchison Bay compared to other sites. Tables 2-4 A and 2-4 B show correlation coefficients as predictors of biometric characteristics of water hyacinth using NO_3-N and SRP concentrations in the surface water, respectively. Significant correlations (*$P = 0.05$; ** $P = 0.01$) indicated that NO_3-N and SRP concentrations had a significant effect on the parameters measured. In addition, negative correlations indicated negative linear relationship between a given parameter with mean concentrations of NO_3-N and SRP, while positive correlations indicated positive linear relationships.

Data on water hyacinth biometrics is given in Figure 2-5. At some sites, some data belong to more than one significant group. Five homogeneous mean leaf length groups

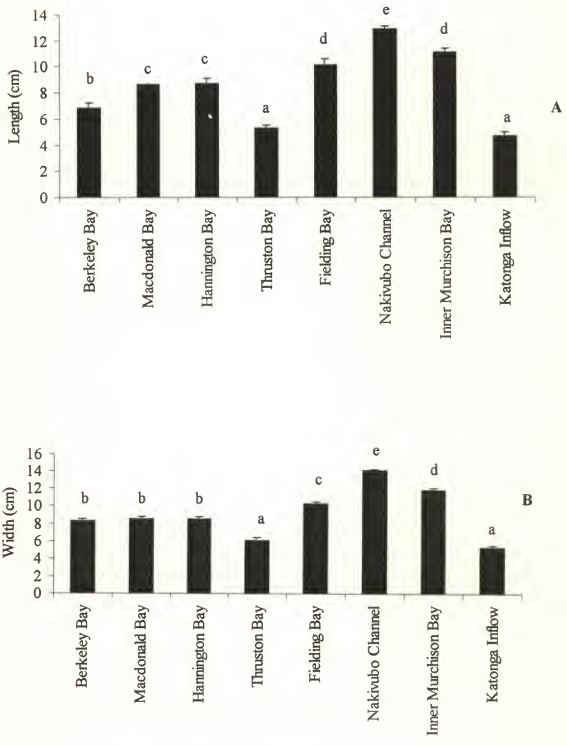


Figure 2-5. Water hyacinth biometrics data from selected bays of Lake Victoria. A) Leaf blade length. B) Leaf blade width. C) Petiole length. D) Root length. Letters above graphs indicate groups that were not significantly different ($P > 0.05$)

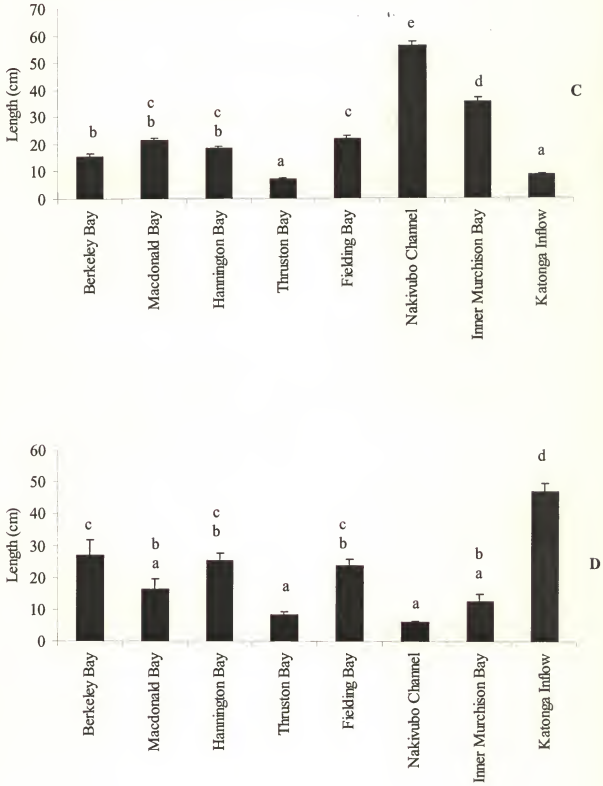


Figure 2-5. Continued

(Figure 2-5 A) that were significantly different (at P = 0.05) were identified. In increasing order, these were from Thruston Bay and Katonga River inflow (range 4.8 to 5.4 cm); Berkeley Bay (range 6.7 to 7.3 cm); Macdonald and Hannington bays (8.7 to 8.8 cm); Fielding and Inner Murchison bays (range 10.2 to 11.2 cm); and the Nakivubo Channel (range 12.7 to 13.1 cm).

Five homogeneous mean leaf width groups (Figure 2-5 B) that were significantly different (at P = 0.05) were identified. In increasing order, they were from the Katonga River inflow and Thruston Bay (range 5.2 to 6.1 cm); Berkeley, Macdonald and Hannington bays (range 8.3 to 8.5 cm); Fielding Bay (10.1 to 10.5 cm); Inner Murchison Bay (11.5 to 12.1 cm); and the Nakivubo Channel (14.1 to 14.3 cm).

There were five homogeneous mean petiole length groups (Figure 2-5 C) that were significantly different (at P = 0.05) from each other. In increasing order, the groupings were from Thruston Bay and Katonga River inflow (range 7.2 to 8.7 cm); Berkeley, Macdonald and Hannington bays (range 15.6 to 21.3 cm); Macdonald, Hannington and Fielding bays (range 18.4 to 22.0 cm); Inner Murchison Bay (34.2 to 37.0 cm); and the Nakivubo Channel (range 54.4 to 57.6 cm).

Four homogeneous mean root length groups (Figure 2-5 D) that were significantly different (at P = 0.05) from each other, were identified. In increasing order, the groupings were from Thruston Bay, Nakivubo Channel and Inner Murchison Bay (range 8.5 to 16.3 cm); Macdonald, Hannington, Fielding and Inner Murchison bays (range 12.6 to 25.5 cm); Berkeley, Hanningtonand Fielding bays (range 23.7 to 26.8 cm); and the Katonga River (range 44.3 to 49.5 cm). Thus, it is in the Nakivubo Channel that the longest and broadest leaf blades, the longest petioles and the shortest roots were found. Stunted

hyacinths were characteristic of the Katonga River inflow and had the shortest and slenderest leaf blades, with some of the shortest bulbous petioles, but with the longest roots.

Physicochemical Limnology during monthly data collection

Physicochemical limnological data taken monthly between May 2001 and June 2002 from field experiments in Inner Murchison, Thruston, and Bunjako Bay are given in Table 2-3. Experiments were not done in Bunjako Bay although monthly limnological data were collected. The cumulative number of measurements (across sites and time) were 60 for both Kisinsi and Bule, 144 for Nakivubo Channel, 27 for Nakivubo open water, 60 for Katonga River inflow, 12 for Katonga open water, 36 for Nkombe, 30 for Thruston open water and 42 for Kafunda.

Mean dissolved oxygen was significantly lower ($P < 0.05$) in the Katonga River inflow and the Nakivubo Channel (range 1.3 to 1.8 mg L^{-1}) compared to the rest of the sites (range 5.7 to 7.7 mg L^{-1}). Significantly lower ($P < 0.05$) water temperatures were characteristic of Katonga River inflow (range 22.0 to 22.4 °C), but the rest of the sites had surface temperatures of > 24 °C, with no significant intersite differences ($P > 0.05$). Both the Katonga River inflow and the Nakivubo Channel were slightly acidic (range 6.4 to 6.9), with pH significantly lower ($P < 0.05$) than at other sites (range 7.4 to 8.9) during the sampling times. Conductivity was significantly higher ($P < 0.05$) in the Nakivubo Channel (range = 322 to 350 μS cm^{-1}), while the other sites, with no significant intersite differences ($P > 0.05$), had conductivity ranging 90 to 120 μS cm^{-1}. All sites were shallow (< 3 m) except the open water site of Thruston Bay. Thus, it was assumed that the water column was well mixed from wave and/or wind action.

Table 2-3. Limnological parameters of surface water

Parameter (Mean ± SE)	Kisinsi	Bule	Nak. Ch.	Mase.	Wan	Kakira	Kat. In.	Bunjako	Nkombe	Thruston Open	Kafunda
D.O. (mgL^{-1})	7.1 ± 0.2	6.8 ± 0.2	1.8 ± 0.2	6.7 ± 0.6	6.9 ± 0.4	6.4 ± 0.6	1.3 ± 0.2	5.9 ± 0.6	7.0 ± 0.4	5.7 ± 0.6	7.7 ± 0.2
Temperature (°C)	26.5 ± 0.2	26.3 ± 0.2	24.9 ± 0.1	26.6 ± 0.2	26.9 ± 0.2	27.5 ± 0.2	22.2 ± 0.2	25.5 ± 0.2	26.9 ± 0.3	26.9 ± 0.2	26.8 ± 0.2
pH	8.2 ± 0.1	8.1 ± 0.1	6.9 ± 0.1	8.7 ± 0.2	8.8 ± 0.2	9.0 ± 0.1	6.4 ± 0.1	7.4 ± 0.2	8.7 ± 0.1	8.6 ± 0.1	8.9 ± 0.1
Conductivity ($\mu S\ cm^{-1}$)	116 ± 6	119 ± 6	336 ± 14	104 ± 2	103 ± 2	107 ± 1	98 ± 2	91 ± 2	103 ± 1	102 ± 1	104 ± 1
Depth (m)	2.5 ± 0.2	1.9 ± 0.1	1.8 ± 0.1	2.1 ± 0.3	1.8 ± 0.3	2.4 ± 0.3	1.1 ± 0.1	2.9 ± 0.2	1.5 ± 0.1	9.9 ± 0.2	2.3 ± 0.1
Number of samples	60	60	144	60	60	60	60	12	36	30	42

Nak. Ch. = Nakivubo Channel; Mase = Masese; Wan. = Wanyange; Kat. In. = Katonga River inflow.

Surface water NO_3-N, SRP, TN and TP during monthly data collection

Ambient nutrient levels in Thruston, Inner Murchison and Bunjako bays are given in Figure 2-6 for NO_3-N, SRP, TN and TP. Across all sampling sites, there were no significant intersite differences ($P > 0.05$) in concentrations of NO_3-N (range 9.4 to 40.7 $\mu g\ L^{-1}$, Figure 2-6 A). Mean concentrations of SRP were in three significantly different ($P < 0.05$) categories; in increasing order, these were Kisinsi, Bule, Nakivubo Open, Masese, Wanyange, Kakira, Bunjako Open, Nkombe, Thruston Open and Kafunda (range 11.2 to 42.3 $\mu g\ L^{-1}$); Katonga River inflow (range 84.0 to 94.6 $\mu g\ L^{-1}$); and the Nakivubo Channel (range 384.2 to 437.4 $\mu g\ L^{-1}$).

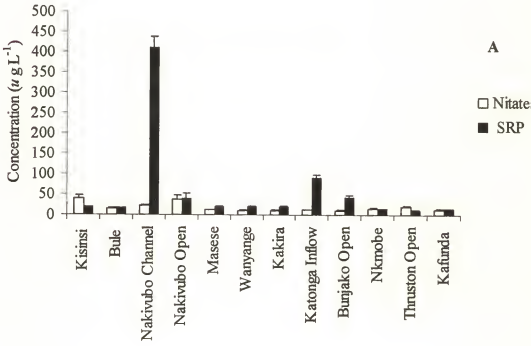


Figure 2-6. N and P concentration in surface waters during Field Experiments. A) NO_3-N and SRP. B) TN and TP.

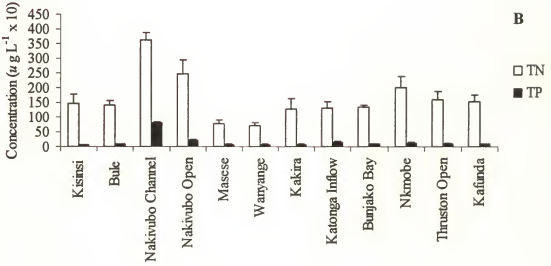


Figure 2-6 Continued

There were no significant intersite differences ($P > 0.05$) in TN concentrations (2-6 B) among sampling sites (range (711.0 to 3,620.7 $\mu g\ L^{-1}$). Total phosphorus was significantly higher ($P < 0.05$) in the Nakivubo Channel (range 753.4 to 841.2 $\mu g\ L^{-1}$). At other sites, TP was significantly lower than in the Nakivubo Channel, but with no intersite differences (range 337.5 to 386.6 $\mu g\ L^{-1}$).

Water Hyacinth Growth Characteristics

Growth characteristics of water hyacinth measured against different concentrations of NO_3-N and SRP during field enclosure growth experiments are given in Figure 2-7, while correlation coefficients between biometrics data and nutrient concentrations are given in Table 2-4. Seven homogeneous groups of leaf blade length were identified ($P < 0.05$) (Figure 2-7 A). Overlaps among the different groups were quite common. In ascending order, the groups were from Nkombe, Bule, Kisinsi, and the Katonga River

inflow (range 3.8 to 4.8 cm); Bule, Kisinsi, the Katonga River inflow, and Kafunda (range 4.1 to 5.2 cm); Kafunda and 600m lakeward of the Nakivubo Channel inflow (range 5.2 to 5.9 cm); at 500 m and 600 m lakeward of the Nakivubo Channel inflow (range 5.9 to 6.3 cm); Nakivubo Channel inflow (range 6.8 to 7.4 cm); 100 m lakeward of the Nakivubo Channel inflow (range 7.9 to 8.5 cm); and at 200 m and 400 m lakeward of the Nakivubo Channel inflow (range 8.7 to 9.2 cm). At all sites except at Nkombe, there were significant positive linear relationships between leaf blade length and NO_3-N concentration in the water (Table 2-4 A). In addition, there were positive linear relationships between leaf blade length and SRP concentrations in the water at all sites except at 500 m lakeward of Nakivubo Channel inflow (Table 2-4 B).

Four homogeneous groups of leaf blade width that were significantly different ($P < 0.05$) were identified (Figure 2-7 B). In ascending order, the groups were from Nkombe and Bule (range 4.4 to 4.8 cm); Katonga River inflow, Kisinsi, and Kafunda (range 5.2 to 6.1 cm); Kisinsi, Kafunda, Nakivubo inflow, and 500 m and 600 m lakeward of the Nakivubo Channel (range 6.0 to 7.1 cm); and 100 m, 200 m and 400 m lakeward of the Nakivubo Channel inflow (range 9.2 to 9.4 cm). At all sites except at the Nakivubo Channel inflow, there were significant positive linear relationships between leaf blade width and NO_3-N concentration in the water (Table 2-4 A). In addition, there were positive linear relationships between leaf blade width and SRP concentrations in the water at all sites (Table 2-4 B).

There were three homogeneous groups of petiole length (Figure 2-7 C) that were significantly different ($P < 0.05$). The groups were from Kisinsi, Bule, Nkombe, Kafunda, Katonga River inflow, and 500 m and 600 m lakeward of the Nakivubo

Table 2-4 A. Correlations between biometric data and NO_3-N concentration in water

Site	Leaf length	Leaf width	Petiole length	Root length
i) Field growth experiments				
Kisinsi	0.607**	0.591**	0.703**	0.944**
Bule	0.796**	0.741**	0.805**	0.942**
Nakivubo Channel Inflow	0.750**	0.958	0.988**	0.938
Nakivubo 100 m Lakeward	0.723**	0.932**	0.975**	0.938**
Nakivubo 200 m Lakeward	0.777**	0.975**	0.941**	0.868**
Nakivubo 300 m Lakeward	0.684**	0.979**	0.994**	0.838**
Nakivubo 400 m Lakeward	0.708**	0.692**	0.730**	0.880*
Nakivubo 500 m Lakeward	0.466*	0.702**	0.642**	0.940**
Nkombe	0.311	0.803**	0.806**	0.679**
Kafunda	0.867**	0.752**	0.837**	0.958**
ii) Semicontrolled growth experiments				
a) Experiment 1				
Control	0.053	0.261	0.252	0.240
Low Level Innoculum	-0.264	0.129	0.085	-0.540**
Medium Level Innoculum	-0.101	-0.071	-0.270	-0.237
High Level Innoculum	-0.290	-0.193	-0.238	-0.230
a) Experiment 2				
Control	-0.128	-0.163	0.167	-0.360
Low Level Innoculum	-0.429**	-0.415**	-0.268	0.161
Medium Level Innoculum	0.072	-0.089	0.199	0.017
High Level Innoculum	0.265	-0.157	0.320*	-0.222

* Significant at $P = 0.05$; ** Significant at $P = 0.01$; Negative correlations are indicated.

Channel inflow (range 5.7 to 9.2 cm); 500 m lakeward of Nakivubo Channel inflow and the Nakivubo Channel inflow (range 9.2 to 11.6 cm); and 100 m, 200 m, and 400 m lakeward of the Nakivubo Channel inflow (range 18.3 to 20.7 cm). At all sites sampled, there were significant positive linear relationships between petiole length and NO_3-N (Table 2-4 A) and SRP (Table 2-4 B) concentration in the water.

Two significantly different ($P < 0.05$) groups of root length were identified (Figure 2-7 D). Significantly longer roots ($P < 0.05$) were at the Katonga River inflow (range 44.3 to 49.5 cm), while the rest of the sites had significantly shorter roots (range 7.2 to 14.1 cm), with shortest roots in the Nakivubo Channel (range 7.2 to 12.2 cm). At

Table 2-4 B. Correlations between biometric data and SRP concentration in water

Site	Leaf length	Leaf width	Petiole length	Root length
i) Field growth experiments				
Kisinsi	0.832**	0.859**	0.911**	0.957**
Bule	0.922**	0.907**	0.958**	0.956**
Nakivubo Channel Inflow	0.963**	0.978**	0.981**	0.905**
Nakivubo 100 m Lakeward	0.933**	0.941**	0.991**	0.962**
Nakivubo 200 m Lakeward	0.979**	0.987**	0.962**	0.914**
Nakivubo 300 m Lakeward	0.939**	0.983**	0.991**	0.776**
Nakivubo 400 m Lakeward	0.663**	0.549**	0.528**	0.855**
Nakivubo 500 m Lakeward	0.306	0.515**	0.467**	0.911**
Nkombe	0.426**	0.715**	0.853**	0.861**
Kafunda	0.876**	0.760**	0.848**	0.970**
ii) Semi-controlled growth experiments				
a) Experiment 1				
Control	0.226	0.272	0.363	-0.213
Low Level Innoculum	0.000	0.058	0.122	-0.088
Medium Level Innoculum	-0.040	0.029	-0.224	0.029
High Level Innoculum	-0.076	-0.094	-0.084	0.010
a) Experiment 2				
Control	-0.006	0.007	0.010	0.410
Low Level Innoculum	-0.263	-0.369*	-0.211	0.088
Medium Level Innoculum	-0.038	-0.185	0.182	0.315
High Level Innoculum	0.133	-0.270	0.399**	-0.259

* Significant at P = 0.05; ** Significant at P = 0.01; Negative correlations are indicated.

Nkombe, Kafunda, Kisnsi, and Bule, roots were equally short as in the Nakivubo Channel, but more numerous per plant than in Nakivubo Channel. It was noted that longest roots were at sites that had low concentrations of either N or P (e.g., the Katonga River inflow) while shortest and fewer roots were in nutrient-rich habitats (e.g., Nakivubo Channel). At all sites except at the Nakivubo Channel inflow, there were significant positive linear relationships between root length and NO_3-N concentration in the water (Table 2-4 A), while effects of SRP concentration on root length were significant at all sites (Table 2-4 B).

Assessment of growth was based on changes, over time, in numbers of ramets (Figure 2-8 A) and leaves (Figure 2-8 B), and wet mass (Figure 2-8 C). In Nakivubo

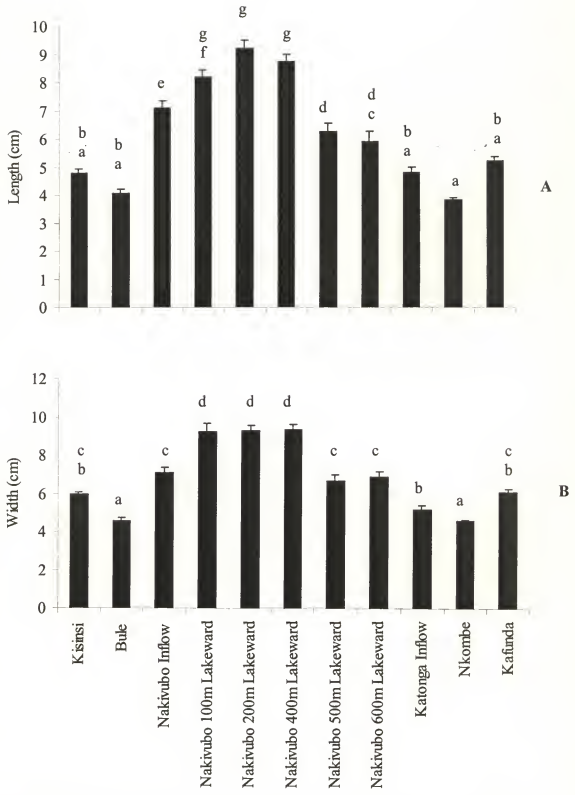


Figure 2-7. Water hyacinth biometrics data from Field Experiments. A) Leaf blade length. B) Leaf blade width. C) Petiole length. D) Root length. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

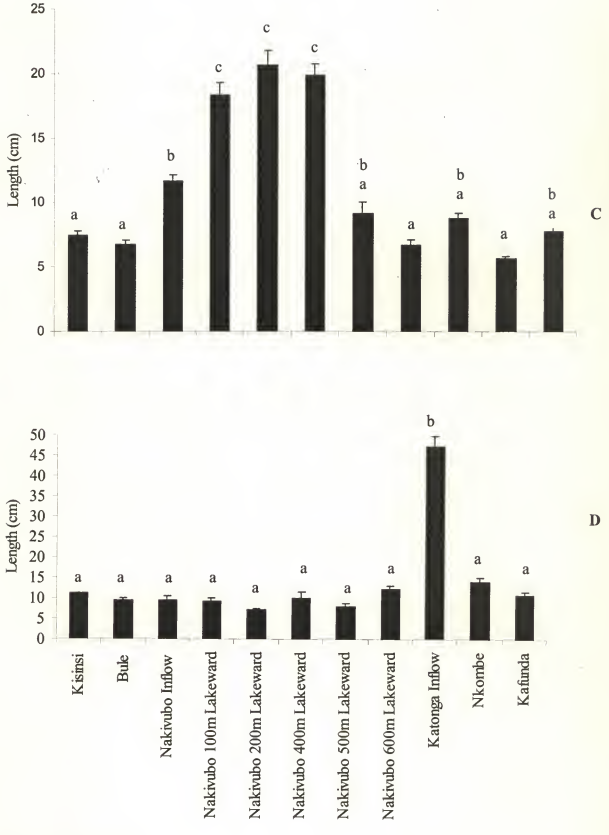


Figure 2-7. Continued

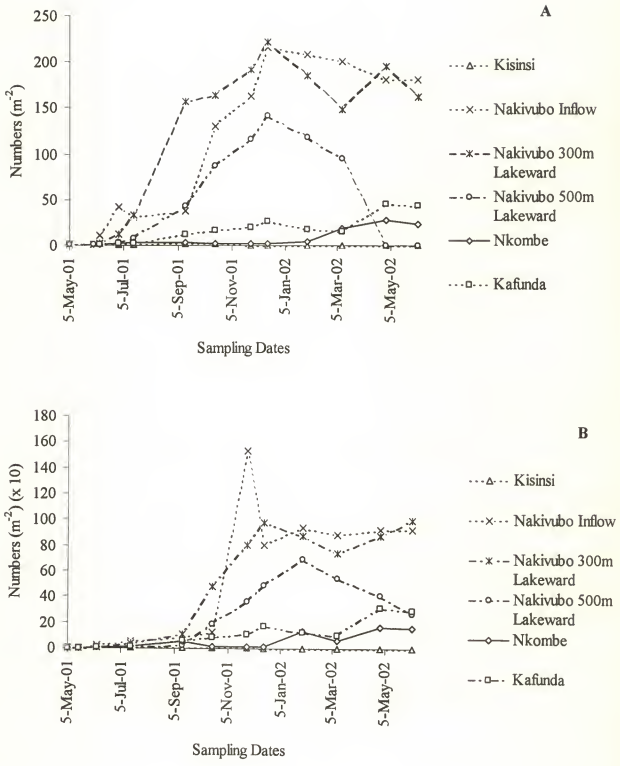


Figure 2-8. Growth parameters of water hyacinth from field experiments. A) Number of ramets. B) Number of leaves. C) Wet mass.

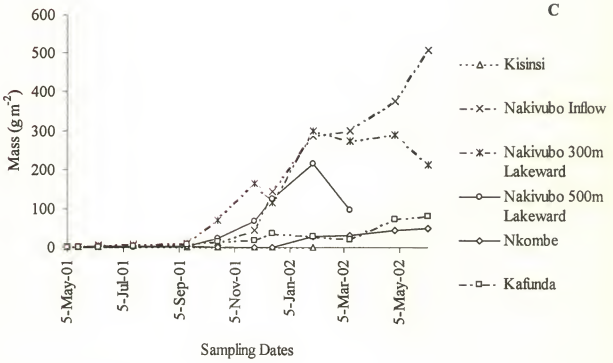


Figure 2-8 Continued.

Channel, increases in numbers of ramets, leaves, and wet mass were exceptionally high until crowding limited production of these growth parameters (Figure 2-8). It should be noted that experimental enclosures were not set in Bunjako Bay and Katonga River inflow. Other than Nakivubo Channel and the Katonga River inflow that were point-sources of nutrients with > 40 $\mu g\ L^{-1}$SRP, other sites in the selected bays had mean SRP of < 20 $\mu g\ L^{-1}$ (Figure 2-6, A). Growth of water hyacinth at such sites was not as rich as observed in Nakivubo Channel. In the Nakivubo Channel, the characteristic sigmoid growth in the number of ramets (Figure 2-8 A) and leaves (Figure 2-8 B), and wet mass (Figure 2-8 C) peaked after 8 months (May to December 2001). In Thruston Bay, growth was not as fast (Figures 2-8 A, B and C) as in the Nakivubo Channel possibly due to low concentrations of NO_3-N and SRP (Figure 2-6 A), coupled with intense feeding by

biological-control weevils. Most field enclosures in Thruston Bay did not attain maximum biomass, and therefore, crowding was not a critical factor in those experiments.

Overall mean number of ramets from onset to termination of the experiments was in three significantly different groups ($P < 0.05$). In ascending order, the groups were Bule, Kisinsi, and 600 m lakeward of the Nakivubo Channel inflow (range 0.7 to 3.4 ramets m^{-2}); Nkombe, Kafunda, 300m, 400 m, and 500 m lakeward of Nakivubo Channel, and Nakivubo Channel inflow (range 8.3 to 113.1 ramets m^{-2}); and at 200 m lakeward of Nakivubo Channel (range 132 to 159.6 ramets m^{-2}). No significant differences ($P > 0.05$) were however, found in specific rate of ramet increase, despite occurrence of higher rates in the Nakivubo Channel (Table 2-5 A). Relative rate of ramet increase (Table 2-5 B) had three homogeneous groups that were significantly different ($p < 0.05$). In ascending order, the groups were from Bule, Kisinsi, 600 m lakeward of the Nakivubo Channel inflow, and Nkombe (range 6.6×10^{-3} to 7.9×10^{-2} ramets day^{-1}); Kafunda, 300 m, 400 m, and 500 m lakeward of the Nakivubo Channel inflow and at the Nakivubo Channel

Table 2-5 A. Specific rates of ramet increase of water hyacinth from enclosure experiments

Site	Specific rate of ramet increase (Numbers Day^{-1})
Kisinsi	6.2×10^{-3}
Bule	6.8×10^{-3}
Nakivubo Inflow	0.1×10^{-2}
200m Lakeward of Nakivubo Inflow	4.7×10^{-2}
300m Lakeward of Nakivubo Inflow	4.6×10^{-2}
400m Lakeward of Nakivubo Inflow	8.0×10^{-2}
500m Lakeward of Nakivubo Inflow	3.7×10^{-2}
600m Lakeward of Nakivubo Inflow	4.9×10^{-2}
Nkombe	2.5×10^{-2}
Kafunda	2.5×10^{-2}

Table 2-5 B. Relative rates of ramet increase of water hyacinth from enclosure Experiments

Site	Relative rate of ramet increase (Numbers Day^{-1})
Kisinsi	$1.1 \times 10^{-2} \pm 3.6 \times 10^{-3}$
Bule	$6.7 \times 10^{-3} \pm 3.6 \times 10^{-3}$
Nakivubo Inflow	1.0 ± 0.3
200m Lakeward of Nakivubo Inflow	1.2 ± 0.3
300m Lakeward of Nakivubo Inflow	1.0 ± 0.2
400m Lakeward of Nakivubo Inflow	0.8 ± 0.2
500m Lakeward of Nakivubo Inflow	0.5 ± 0.1
600m Lakeward of Nakivubo Inflow	$3.5 \times 10^{-2} \pm 2.7 \times 10^{-2}$
Nkombe	$7.9 \times 10^{-2} \pm 1.7 \times 10^{-2}$
Kafunda	$0.2 \pm 2.1 \times 10^{-2}$

inflow (range 0.2 to 1.0 ramets day^{-1}); and all data from the latter category including 200 m lakeward of the Nakivubo Channel (range 0.2 to 1.2 ramets day^{-1}). The concentrations of NO_3-N and SRP in the water, through regression, did not significantly predict the rate of ramet increase (Tables 2-6 A and B, respectively). Some data on rate of ramet increase may not be reliable since water hyacinth populations in some enclosures were not stable in unsheltered sites of Bule and Kisinsi and at 500 m and 600 m lakeward from the Nakivubo Channel inflow. Some ramets were flushed out of the enclosures during rough weather characterized by strong waves and winds. It was expected that highest rate of ramet increase would be at the inflow of the Nakivubo Channel, but this was not the case, implying that highest availability of nutrients may not necessarily correspond to highest rate of ramet increase.

Overall mean number of leaves from onset to termination of the experiments was in three significantly different groups ($P < 0.05$). In ascending order, the groups were Bule, Kisinsi, and 600 m lakeward of the Nakivubo Channel inflow, and Nkombe (range 2.6 to 59.5 leaves m^{-2}); Kafunda, 400 m, and 500 m lakeward of Nakivubo Channel (range 117.7 to 352.2 leaves m^{-2}); and at 200 m and 300 m lakeward of Nakivubo Channel, and

Nakivubo inflow (range 493.4 to 5,24.6 leaves m^{-2}). No intersite significant differences were noted in both specific (range -5.1×10^{-2} to 6.9×10^{-2} leaves day^{-1}), and relative (range 4.8×10^{-3} to 1.0 leaves day^{-1}) rate of leaf recruitment (Tables 2-5 C and D). There was no significant effect of NO_3-N concentration in the water on both specific and relative rates of leaf recruitment when predicted using regression analysis (Table 2.6 A).

Table 2-5 C. Specific rates of leaf recruitment of water hyacinth from enclosure Experiments

Site	Specific rate of leaf recruitment (Numbers Day^{-1})
Kisinsi	$-3.4 \times 10^{-3} \pm 6.3 \times 10^{-3}$
Bule	$-5.1 \times 10^{-3} \pm 5.7 \times 10^{-3}$
Nakivubo Inflow	$6.9 \times 10^{-2} \pm 4.5 \times 10^{-2}$
200m Lakeward of Nakivubo Inflow	$5.8 \times 10^{-2} \pm 4.5 \times 10^{-2}$
300m Lakeward of Nakivubo Inflow	$3.2 \times 10^{-2} \pm 1.3 \times 10^{-2}$
400m Lakeward of Nakivubo Inflow	$4.2 \times 10^{-2} \pm 2.5 \times 10^{-2}$
500m Lakeward of Nakivubo Inflow	$2.8 \times 10^{-2} \pm 1.6 \times 10^{-2}$
600m Lakeward of Nakivubo Inflow	$3.0 \times 10^{-2} \pm 3.4 \times 10^{-2}$
Nkombe	$2.5 \times 10^{-2} \pm 2.4 \times 10^{-2}$
Kafunda	$3.3 \times 10^{-2} \pm 9.4 \times 10^{-3}$

Table 2-5 D. Relative rates of leaf recruitment of water hyacinth from enclosure Experiments

Site	Relative rate of leaf recruitment (Numbers Day^{-1})
Kisinsi	$4.8 \times 10^{-3} \pm 2.2 \times 10^{-3}$
Bule	$4.8 \times 10^{-3} \pm 2.5 \times 10^{-3}$
Nakivubo Inflow	1.0 ± 0.3
200m Lakeward of Nakivubo Inflow	0.9 ± 0.2
300m Lakeward of Nakivubo Inflow	0.9 ± 0.2
400m Lakeward of Nakivubo Inflow	0.7 ± 0.2
500m Lakeward of Nakivubo Inflow	0.4 ± 0.1
600m Lakeward of Nakivubo Inflow	$2.2 \times 10^{-2} \pm 1.8 \times 10^{-2}$
Nkombe	$0.1 \pm 2.2 \times 10^{-2}$
Kafunda	$0.2 \pm 2.7 \times 10^{-2}$

Similar observations were noted for SRP concentration in the water at all sites except at 300 m lakeward of the Nakivubo Channel inflow where a significant regression (r^2 = 0.73) was noted (Table 2-6 B).

Biomass increase over time was based on cumulative wet mass. No significant differences ($P > 0.05$) were noted in wet mass specific (range -8.4×10^{-3} to 0.1 g day^{-1}), and wet mass relative (range 2.0×10^{-3} to 1.2 g day^{-1}) growth rates among sites (Tables 2-5 E and F). In addition, concentrations of NO_3-N, and of SRP in the water did not have significant effects on growth rates of water hyacinth at all sites (Tables 2-6 A and B).

Table 2-5 E. Specific rates of growth (wet mass) of water hyacinth from selected sites

Site	Specific rate of mass increase (g day^{-1})
Kisinsi	$-3.9 \times 10^{-3} \pm 6.9 \times 10^{-3}$
Bule	$-8.4 \times 10^{-3} \pm 6.6 \times 10^{-3}$
Nakivubo Inflow	$5.3 \times 10^{-2} \pm 2.7 \times 10^{-2}$
200m Lakeward of Nakivubo Inflow	$4.5 \times 10^{-2} \pm 2.2 \times 10^{-2}$
300m Lakeward of Nakivubo Inflow	$4.3 \times 10^{-2} \pm 2.1 \times 10^{-2}$
400m Lakeward of Nakivubo Inflow	$7.3 \times 10^{-2} \pm 6.0 \times 10^{-2}$
500m Lakeward of Nakivubo Inflow	$4.0 \times 10^{-2} \pm 3.0 \times 10^{-2}$
600m Lakeward of Nakivubo Inflow	$1.6 \times 10^{-2} \pm 1.8 \times 10^{-2}$
Nkombe	$0.1 \pm 9.5 \times 10^{-2}$
Kafunda	$2.6 \times 10^{-2} \pm 1.2 \times 10^{-2}$

Table 2-5 F. Relative rates of growth (wet mass) of water hyacinth from enclosure Experiments

Site	Relative rate of wet mass increase (g day^{-1})
Kisinsi	$6.0 \times 10^{-3} \pm 4.3 \times 10^{-3}$
Bule	$2.0 \times 10^{-3} \pm 3.8 \times 10^{-3}$
Nakivubo Inflow	1.0 ± 0.3
200m Lakeward of Nakivubo Inflow	1.2 ± 0.3
300m Lakeward of Nakivubo Inflow	1.1 ± 0.3
400m Lakeward of Nakivubo Inflow	0.7 ± 0.2
500m Lakeward of Nakivubo Inflow	0.3 ± 0.1
600m Lakeward of Nakivubo Inflow	$1.7 \times 10^{-2} \pm 1.5 \times 10^{-2}$
Nkombe	$6.2 \times 10^{-2} \pm 2.4 \times 10^{-2}$
Kafunda	$0.2 \pm 8.3 \times 10^{-2}$

Table 2-6 A. Regression between NO_3-N concentration in the water and growth parameters of water hyacinth in enclosure experiments

Site/Experiment	Specific rate of ramets increase	Specific rate of increase in leaf population	Wet mass specific growth rate	Wet mass relative growth rate
i) Experimental enclosures				
Kisisni	0.081	0.436	0.035	0.002
Bule	0.408	0.194	0.004	0.002
Nakivubo Inflow	0.013	0.008	0.004	0.060
200m Lakeward of Nakivubo Inflow	0.080	0.062	0.000	0.033
300m Lakeward of Nakivubo Inflow	0.161	0.132	0.154	0.068
400m Lakeward of Nakivubo Inflow	0.125	0.124	0.000	0.046
500m Lakeward of Nakivubo Inflow	0.256	0.205	0.021	0.019
600m Lakeward of Nakivubo Inflow	0.266	0.331	0.432	0.009
Nkombe	0.000	0.060	0.011	0.019
Kafunda	0.046	0.104	0.153	0.060

Table 2-6 B. Regression between SRP concentration in the water and growth parameters of water hyacinth in enclosure experiments

Site/Experiment	Specific rate of ramet increase	Specific rate of increase in leaf population	Wet mass specific growth rate	Wet mass relative growth rate
i) Experimental enclosures				
Kisisni	0.000	0.111	0.116	0.087
Bule	0.005	0.181	0.120	0.003
Nakivubo Inflow	0.164	0.005	0.000	0.071
200m Lakeward of Nakivubo Inflow	0.378	0.076	0.001	0.100
300m Lakeward of Nakivubo Inflow	0.011	0.729**	0.318	0.184
400m Lakeward of Nakivubo Inflow	0.077	0.392	0.016	0.213
500m Lakeward of Nakivubo Inflow	0.241	0.104	0.016	0.172
600m Lakeward of Nakivubo Inflow	0.196	0.046	0.035	0.244
Nkombe	0.003	0.181	0.271	0.191
Kafunda	0.011	0.012	0.085	0.328

** Significant at P = 0.01 for both Tables 2-6 A and 2-6 B

Specific growth rate (SGR) converted to doubling time (D_t) is given in Figure 2-9. There was a significant ($P = 0.01$) inverse correlation ($r = -0.899$) between doubling time and SGR. Thus, doubling time was lowest in nutrient-rich sites but highest in relatively nutrient-poor habitats.

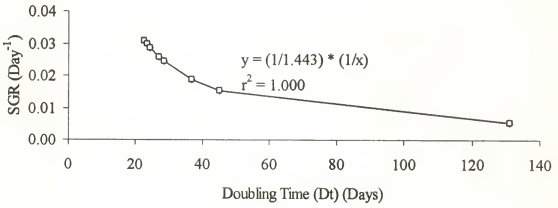


Figure 2-9. Specific Growth Rate of water hyacinth converted to Doubling Time (Dt).

Root:shoot ratios (R:S) based on ash-free dry weight and carbon content of water hyacinths from selected bays of Lake Victoria are given in Table 2-7. Significantly higher ($P < 0.05$) mean biomass R:S were found in Macdonald Bay, the Katonga River inflow, and the Kagera River (range 1.64 to 4.67). At other sites, differences were not significant (range 0.19 to 1.47). Differences in R:S based on carbon content were not significantly different ($P > 0.05$) among sites (range 0.14 to 2.62). High R:S ratios were associated with nutrient-poor environments where an extensive root system increases the absorptive surface for nutrients.

Table 2-7. Root:shoot ratios (R:S) from selected bays of Lake Victoria and from semicontrolled experiments

Bay	Site	Biomass R:S	Carbon R:S	n
Berkeley	Sio River Inflow & Buchunia	1.47 ± 0.16	0.78 ± 0.22	14
Macdonald	Bugoto	1.64 ± 0.42*	0.96 ± 0.39	14
Hannington	Lwanika	1.00 ± 0.14	0.74 ± 0.20	8
Thruston	Nkombe-Kafunda	0.95 ± 0.30	0.62 ± 0.10	20
Fielding	Masese-Wanyange	0.77 ± 0.14	0.47 ± 0.10	15
Murchison	Nakivubo Channel Inflow	0.26 ± 0.04	0.17 ± 0.03	13
	200m Lakeward Nakivubo Inflow	0.83 ± 0.17	1.03 ± 0.90	10
	300m Lakeward Nakivubo Inflow	0.19 ± 0.08	0.14 ± 0.02	13
	400m Lakeward Nakivubo Inflow	0.22 ± 0.02	0.14 ± 0.06	11
	600m Lakeward Nakivubo Inflow	0.66 ± 0.17	0.28 ± 0.05	10
	Kisinsi-Bule	0.46 ± 0.08	0.36 ± 0.04	18
Bunjako	Katonga River Inflow	1.73 ± 0.23*	1.17 ± 0.19	18
	Katebo	0.65 ± 0.13	0.42 ± 0.06	14
Kasensero	Kagera River	4.67 ± 2.01*	2.62 ± 1.52	13
Experiments	Control	0.47 ± 0.18	0.72 ± 0.20	12
	Low-level Innoculum	0.47 ± 0.14	0.72 ± 0.18	12
	Medium-level Innoculum	0.39 ± 0.09	0.76 ± 0.03	12
	High-level Innoculum	0.84 ± 0.09	0.79 ± 0.08	12

* Significantly higher ($P < 0.05$)

Water Hyacinth Growth under Semicontrolled Laboratory Conditions

Average concentrations of NO_3-N and SRP of replicates over time for Experiments 1 and 2 are given in Figure 2-10. Nutrients were inoculated into experimental tanks tank for Experiments 1 and 2, respectively. The aim of varying the inoculations was to attain a minimum concentration of nutrients that would result in minimum plant growth. In Experiment 1, all treatments were significantly different ($P < 0.05$) from each other with respect to NO_3-N, averaging 125.6 ± 6.8 μg L^{-1} in the control, 373.2 ± 16.9 μg L^{-1} in the low, 584.2 ± 47.4 μg L^{-1} medium, and 782.9 ± 57.5 μg L^{-1} in the high-level treatments. In Experiment 2, NO_3-N concentrations in the control and the low-level treatment (range 121.7 to 202.4 μg L^{-1}) were not significantly different ($P > 0.05$), while the latter was not significantly different from the medium-level treatment (range 191.5 to 253.9 μg L^{-1}).

Significantly higher NO_3-N in Experiment 2 was in the high-level treatment (351.3 ± 12.3 μg L^{-1}). Dilution of innocula from the level in Experiment 1 to Experiment 2 decreased NO_3-N by 52.9 % in the low (i.e., from 373.2 ± 16.9 μg L^{-1} to 175.9 ± 26.5 μg L^{-1}),

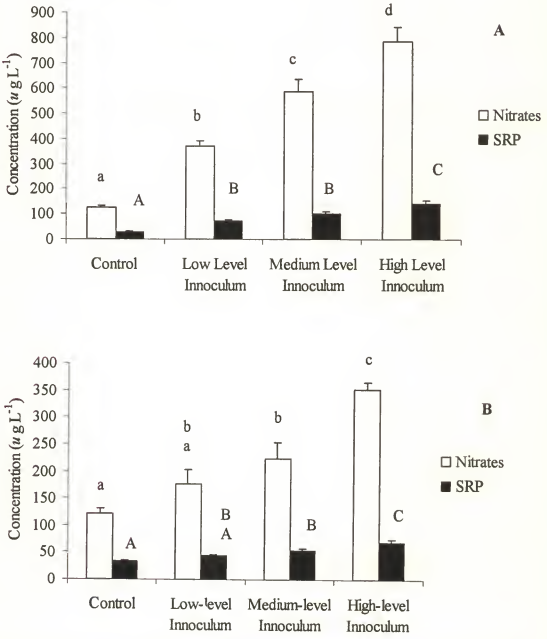


Figure 2-10. Concentrations of NO_3-N and SRP in experimental tanks (note differences in scale between Graphs A and B). A) Experiment 1, B) Experiment 2. Letters above graphs indicate groups that are not significantly different ($P > 0.05$). Upper case letters are for SRP; lower case for NO_3-N.

61.9 % in the medium (from 584.2 ± 47.4 μg L^{-1} to 222.7 ± 31.2 μg L^{-1}), and 55.1 % (from 782.9 ± 57.5 μg L^{-1} to 351.3 ± 12.3 μg L^{-1}) in the high-level treatments. There was a slight decrease in concentration of NO_3-N (3.1 %) in the control setup.

Average concentrations of SRP in Experiment 1 were significantly lower ($P < 0.05$) in the control (29.8 ± 2.0 μg L^{-1}), and significantly higher ($P < 0.05$) in the high-level treatment (142.3 ± 11.9 μg L^{-1}). Mean concentrations of SRP in the low and medium level treatments (range 71.6 to 99.4 μg L^{-1}) were not significantly different ($P > 0.05$), but were significantly lower than the high level treatment, and significantly higher than the control setup. In Experiment 2, SRP concentrations were significantly lower ($P < 0.05$) in the control setup and the low-level treatment (range 32.2 to 47.3 μg L^{-1}), but concentrations in the latter were not significantly different ($P > 0.05$) from the medium-level treatment (54.5 ± 3.4 μg L^{-1}). Significantly higher ($P < 0.05$) SRP concentrations were in the high-level treatment (70.1±4.9 μg L^{-1}). Dilution of innocula from that in Experiment 1 to Experiment 2 resulted in a SRP decrease by 37.8 % (i.e., from 71.6 ± 5.2 μg L^{-1} to 44.5 ± 2.8 μg L^{-1}) in the low-level treatment, 45.2 % (i.e., from 99.4 ± 8.5 μg L^{-1} to 54.5 ± 3.4 μg L^{-1}) in the medium-level, and 50.7 % (i.e., from 142.3 ± 11.9 μg L^{-1} to 70.1 ± 4.9 μg L^{-1}) in the high-level treatment. An increase of SRP in the control setup by 14.8 % (i.e. from 29.7 ± 2.0 μg L^{-1} in Experiment 1 to 34.2 ± 1.8 μg L^{-1} in Experiment 2) was attributed to contamination of the experimental tanks possibly from flying insects.

In both experiments, N:P ratios were not limiting to plant growth since they were in the range (2.3 to 5.0) considered optimum for growth (Sato and Kondo 1981; Reddy and Tucker 1983). In Experiments 1 and 2, respectively, N:P ratios were 4.2 and 3.6 for the

control setup, 5.2 and 4.0 for the low-level treatment, 5.9 and 4.1 for the medium-level treatment, and 5.5 and 5.0 for the high-level treatment. Ratios above 5.0 indicated slightly excess N.

Graphical data reported on number of ramets and leaves, and wet mass are from Experiment 1, while relative growth rate (RGR) are for both Experiments 1 and 2. Cumulative numbers of ramets (Figure 2-11 A) and leaves (Figure 2-11 B) and wet mass (Figure 2-11 C) greatly increased in all treatments except the control. All growth parameters assessed exhibited positive growth except the control, where no remarkable increase occurred in either numbers of ramets and leaves or wet mass.

There were no significant treatment effects ($P > 0.05$) on specific rate of ramet recruitment in both Experiment 1 (range 1.1×10^{-2} to 7.7×10^{-2} day^{-1}), and Experiment 2 (range 1.1×10^{-2} to 0.2 day^{-1}). In Experiment 1, relative rate of ramet recruitment was significantly lower ($P < 0.05$) in the control setup (8.0×10^{-3} day^{-1}), but no significant differences occurred among the rest of the treatments (range 0.1 to 0.2 day^{-1}). In Experiment 2, there were no significant differences in relative rates of ramet recruitment among treatments and the control (range 8.6×10^{-3} to 0.3 day^{-1}). In Experiment 1, regression between specific rate of ramet recruitment and NO_3-N (Table 2-8 A) was not significant in all trials, except for the low-level treatment ($r^2 = 0.79$). Additionally, no significant regression was noted between specific rate of ramet increase and NO_3-N (Table 2-8 A) in all trials. No significant regression was noted between rates of ramet recruitment and SRP concentration in the water in all trials of both Experiments 1 and 2 (Tables 2-8 A and B).

In Experiment 1, specific rates of leaf recruitment were in three significantly homogeneous groups. Lowest specific rate was in the control setup ($8.6 \times 10^{-3} \pm 6.5 \times 10^{-3}$ day^{-1}), while highest was in the high-level treatment ($3.6 \times 10^{-2} \pm 6.1 \times 10^{-3}$ day^{-1}).

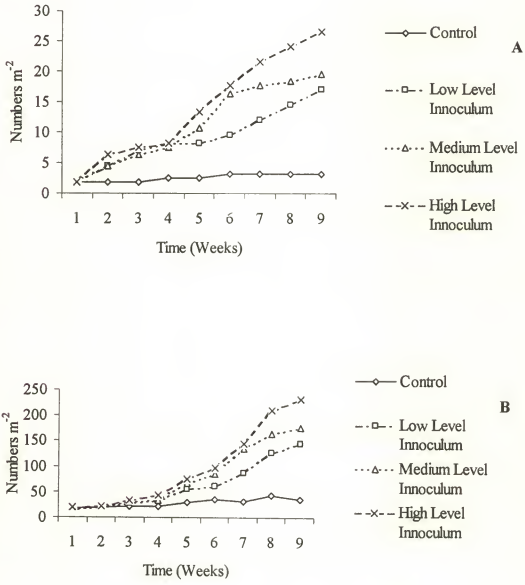


Figure 2-11. Growth parameters of water hyacinth from semicontrolled Experiment 1. Cumulative increase in A) Ramets, B) Leaves, and C) Wet mass

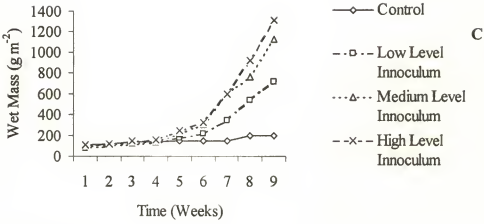


Figure 2-11. Continued

Table 2-8 A. Regression between NO_3-N concentration in water and growth parameters of water hyacinth semicontrolled experiments

Site/Experiment	Specific rate of ramets increase	Specific rate increase in leaf population	Wet mass specific growth rate	Wet mass relative growth rate
a) Experiment 1				
Control	0.533	0.005	0.087	0.029
Low level innoculum	0.794**	0.071	0.186	0.162
Medium level innoculum	0.112	0.110	0.025	0.052
High level innoculum	0.152	0.045	0.016	0.031
b) Experiment 2				
Control	0.391	0.003	0.482	0.692
Low level innoculum	0.000	0.004	0.085	0.682
Medium level innoculum	0.001	0.000	0.026	0.733
High level innoculum	0.493	0.102	0.192	0.016

** Significant at P = 0.01

Specific leaf recruitment rates in the low-level, and medium-level treatments (range 3.0 x 10^{-2} to 3.2 x 10^{-2} day-1) were not significantly different from each other, nor from the control setup and the high-level treatment. In Experiment 2, there were no significant differences ($P > 0.05$) in specific rates of recruitment of leaves (range 1.5 x 10^{-2} to 7.2 x

10^{-2} day^{-1}). Regression between specific rates of leaf recruitment and nutrient concentrations (NO_3-N and SRP) was not significant (Tables 2-8 A and B).

Table 2-8 B. Regression between SRP concentration in water and growth parameters of water hyacinth semicontrolled experiments

Site/Experiment	Specific rate of ramets increase	Specific rate increase in leaf population	Mass specific growth rate	Mass relative growth rate
a) Experiment 1				
Control	0.002	0.284	0.306	0.837**
Low level innoculum	0.315	0.346	0.169	0.085
Medium level innoculum	0.441	0.128	0.059	0.016
High level innoculum	0.339	0.162	0.009	0.003
b) Experiment 2				
Control	0.095	0.000	0.223	0.178
Low level innoculum	0.049	0.085	0.076	0.453
Medium level innoculum	0.000	0.005	0.006	0.935**
	0.109	0.018	0.135	0.803**

** Significant at P = 0.01

Relative rates of leaf recruitment for Experiment 1 were significantly lower ($P < 0.05$) in the control setup ($1.6 \times 10^{-2} \pm 1.7 \times 10^{-3}$ day^{-1}), while it was significantly higher in all treatments (range 5.7×10^{-2} to 7.8×10^{-2} day^{-1}). Relative rates of leaf recruitment for Experiment 2 were significantly lower ($P < 0.05$) in the control setup, and the low-level treatment (range 2.2×10^{-2} to 8.8×10^{-2} day^{-1}), while it was significantly higher in the medium and high-level treatments (range 0.1 to 0.2 day^{-1}).

Cumulative wet mass was significantly lower ($P < 0.05$) in the control setup, while no significant differences occurred among treatments (Figure 2-11 C). Plants in the control setup were chlorotic, with bunches of dying roots, while their live roots were purple in color.

Relative growth rates (RGR) for Experiments 1 and 2 are given in Figures 2-12 A and B, respectively. In Experiment 1, no significant differences ($P > 0.05$) in RGR were noted among treatments (range 4.8×10^{-2} to 5.2×10^{-2} day^{-1}), while it was significantly lower ($P < 0.05$) in the control ($1.2 \times 10^{-2} \pm 1.6 \times 10^{-3}$ day^{-1}). Similar observations were made in Experiment 2, with significantly lower ($P < 0.05$) RGR in the control (1.5 x 10-2 ± 1.3 x 10-3 day), while in the low, medium, and high level treatments, RGR were not significantly different ($P > 0.05$) from each other (range 8.0×10^{-2} to 0.1 day^{-1}), but were significantly higher than the control setup.

Doubling time (D_t), on the other hand, decreased with increased nutrient concentrations in experimental tanks. In Experiment 1, significantly higher ($P < 0.05$) D_t (1967 days) was in the control, while there were no significant differences among treatments (range 25 to 28 days). In Experiment 2, Dt was also significantly higher in the Control setup (6,444 days), while no significant differences ($P > 0.05$) occurred among treatments (range 19 to 27 days).

Efficiency ratios, a measure of how efficiently plants accumulate nutrients in their tissues, are given in Table 2-9 for various plant parts in relation to TN and TP. Mean TN efficiency ratios in leaves were significantly lower ($P < 0.05$) in plants from the high level treatment ($0.7 \pm 2.9 \times 10^{-3}$ percent dry wt.), while they were significantly higher in leaves from the medium level treatment ($1.0 \pm 3.5 \times 10^{-2}$ percent dry wt.). Ratios in leaves from the control setup, and the low-level treatment (range 0.8 to 0.9 percent dry wt.) were not significantly different from the first two groups. No significant differences ($P > 0.05$) were noted in TP efficiency ratios in leaves among all trials (range 8.0×10^{-2} to 0.1 percent dry wt.).

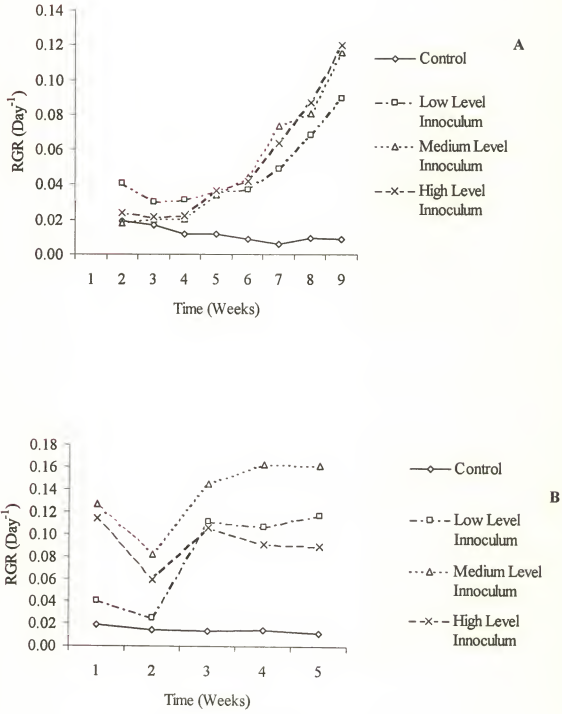


Figure 2-12. Relative growth rates (RGR) of water hyacinth under semicontrolled conditions. A) Experiment 1; B) Experiment 2.

Mean TN efficiency ratios in petioles were significantly lower ($P < 0.05$) in plants from the medium level treatment ($0.7 \pm 3.5 \times 10^{-2}$ percent dry wt.), while they were significantly higher in leaves from the control setup (4.0 ± 1.0 percent dry wt.). Ratios in petioles from the low and high level treatments (range 1.8 to 1.9 percent dry wt.) were not significantly different from the first two groups. No significant differences ($P > 0.05$) were noted in TP efficiency ratios in petioles among trials (range 0.1 to 0.2 percent dry wt.).

There were no significant differences ($P > 0.05$) in TN efficiency ratios among rhizomes from all trials (range 0.5 to 3.2 percent dry wt.). Of the TP efficiency ratios, significantly lower ($P < 0.05$) values were in rhizomes from the low, medium, and high-level treatments (range 9.0×10^{-2} to 0.1 percent dry wt.), while significantly higher values were from the control setup (0.5 ± 0.2 percent dry wt.).

Efficiency ratios (reciprocal of tissue nutrient concentrations) for TN in roots was significantly lower ($P < 0.05$) among all treatments (range 0.9 to 1.3 percent dry wt.), while they were significantly higher in roots from the control setup (2.0 ± 0.2 percent dry wt.). There were no significant differences ($P > 0.05$) in efficiency ratios for TP in roots among all trials.

Table 2-9. Efficiency ratios (percent dry wt.) by water hyacinth plants under semicontrolled conditions

Nutrient	Plant parts	Control	Low Level Innoculum	Medium Level Innoculum	High Level Innoculum
a) TN	Leaves	0.83	0.86	0.98	0.72
	Petioles	4.01	1.95	0.68	1.81
	Rhizomes	1.67	3.19	1.21	0.47
	Roots	1.97	1.33	1.13	0.85
b) TP	Leaves	0.11	0.09	0.11	0.08
	Petioles	0.20	0.14	0.19	0.13
	Rhizomes	0.50	0.10	0.14	0.09
	Roots	0.22	0.20	0.20	0.15

Biometrics Data of Plants from Semicontrolled Experiments

Biometrics data of plants from semicontrolled Experiment 2 are given in Figure 2-13. Three mean leaf blade length groups were identified (Figure 2-13 A). Leaf blades with significantly shorter ($P < 0.05$) length were from the control setup and the low-level treatment (range 2.9 to 3.1 cm). Leaf length from the low and medium-level treatments were not significantly different from each other (range 3.1 to 3.2 cm), while those from the medium and high-level treatments had longer ($P < 0.05$) leaves (range 3.2 to 3.5 cm).

Leaf blade width occurred in two significantly different ($P < 0.05$) homogeneous groups (Figure 2-13 B). The slenderest leaves were from the control setup (range 3.9 to 4.1 cm), while the broadest leaves were from all treatments (range 4.6 to 4.9 cm).

Three significantly different ($P < 0.05$) homogeneous groups of petiole length were identified (Figure 2-13 C). Significantly shorter petioles were from the control setup (range 3.9 to 4.3 cm), while significantly longer petioles were in the high-level treatment (range 5.0 to 5.3 cm). The third group was with petioles that were significantly longer than the control group, but significantly shorter than the high-level treatment group. This third group, with no intertreatment differences, was from the low and medium-level treatments (range 4.5 to 4.7 cm).

Root length, though given in Figure 2-13 D, may not be representative of response to nutrients since both old and new roots occurred on the same plant. Despite this, available data indicated two significantly different groups, with shortest roots occurring in the control setup, while longest in the high-level treatment. Length in the low and medium-level treatments did not differ from the first two groups.

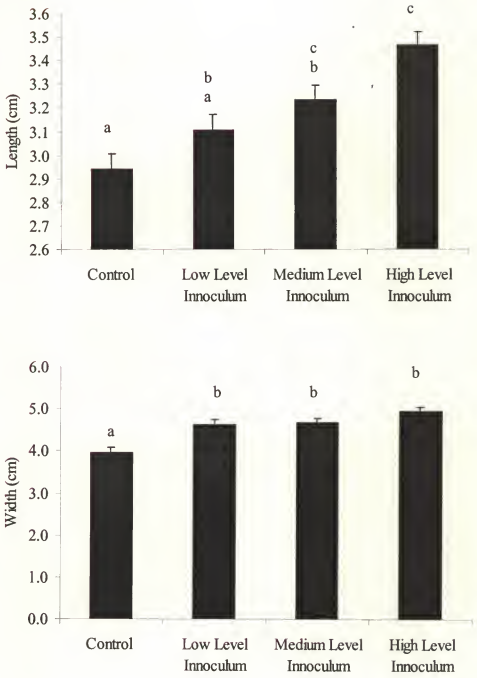
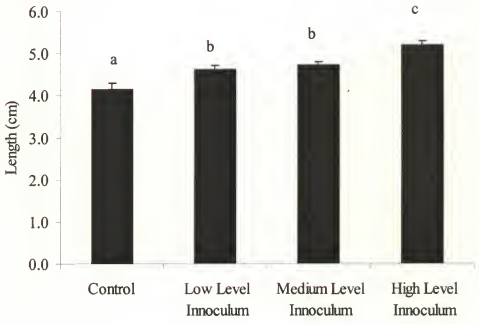


Figure 2-13. Biometrics data of water hyacinth from the semicontrolled Experiment 2. A) Leaf-blade length. B) Leaf-blade width. C) Petiole length. D) Root length. Letters above graphs indicate groups that are significantly similar.



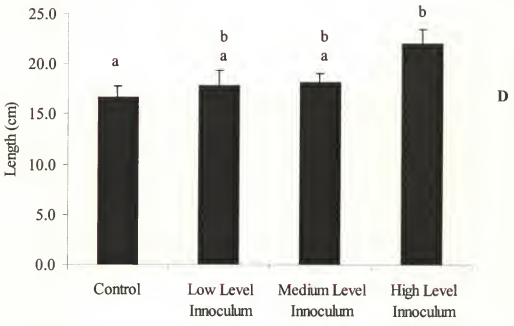


Figure 2-13. Continued.

Concentration of N and P in Tissues of Water Hyacinths

Concentration of TN in plant parts from Semicontrolled Experiments

Total nitrogen (TN as per cent dry wt.) in various plant parts from different treatments is given in Figure 2-14. Two homogeneous groups of TN concentration ($P < 0.05$) in leaves were identified (Figure 2-14 A). Significantly lower mean concentrations were in leaves from the medium-level treatment (range 0.97 to 1.09 percent dry wt.), while significantly higher mean concentrations were in leaves from high-level treatments (range 1.33 to 1.43 percent dry wt.). Mean concentrations of TN in leaves from the control setup, and the low-level treatment were not significantly different from each other (range 1.12 to 1.25 percent dry wt.), neither were they significantly different from leaves in the medium, and high-level treatments.

Among petioles, two groups of mean concentrations of TN were identified (Figure 2-14 B). Significantly lower ($P < 0.05$) mean values were in petioles from the control setup (range 0.26 to 0.38 percent dry wt.), while significantly higher mean concentrations were in the medium-level treatments (range 1.39 to 1.53 percent dry wt.). Mean concentrations of TN in petioles from the low and high-level treatments were not significantly different (range 0.52 to 0.55 percent dry wt.), and were not significantly different from that in the control setup and the medium-level treatment.

Mean TN concentrations in rhizomes (Figure 2-14 C) were in two significantly different ($P < 0.05$) homogeneous groups. Significantly lower TN ($P < 0.05$) was in rhizomes from the control setup, and the low and medium-level treatments (range 0.63 to 0.83 percent dry wt.). Mean TN in rhizomes was significantly higher among plants from the high level treatments (range 1.66 to 2.94 percent dry wt.).

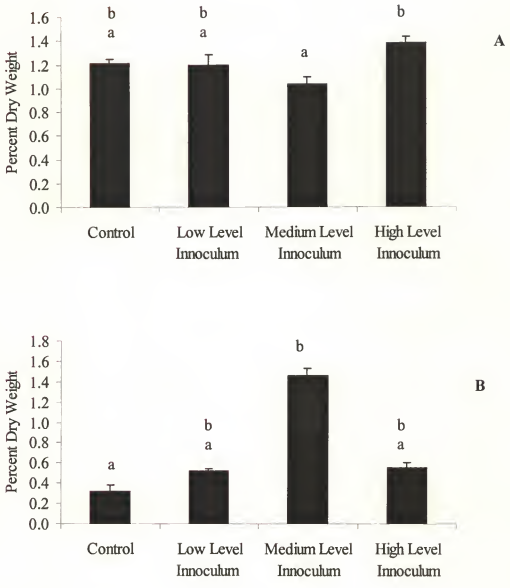


Figure 2-14. TN content in plant parts from semicontrolled experiments. A) Leaves. B) Petioles. C) Rhizomes. D) Roots. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

Three significantly different ($P < 0.05$) homogeneous groups of mean TN concentration in roots were identified (Figure 2-14 D). Significantly lower TN was in roots from the control setup (range 0.49 to 0.57 percent dry wt.), while significantly higher TN was in the high-level treatment (range 1.83 to 1.95 percent dry wt.). Average concentrations of TN in roots from the low, and medium-level treatments were not

significantly different from each other (range 0.78 to 0.89 percent dry wt.), and were not significantly different from the control setup.

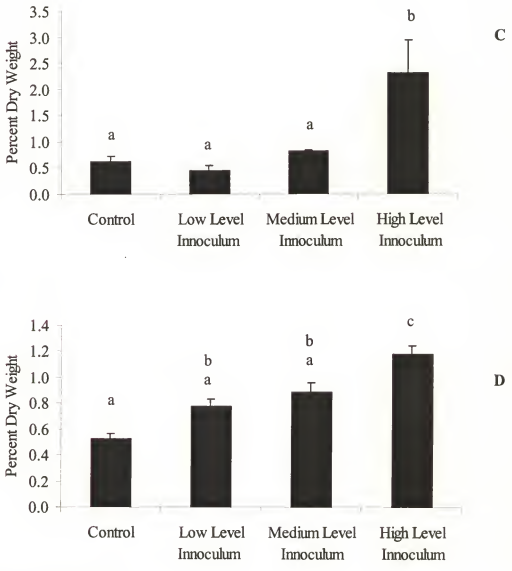


Figure 2-14. Continued

Concentration of TP in plant units from Semicontrolled Experiments

Concentration of TP (per cent dry wt.) in plant parts from different experimental tanks is given in Figure 2-15. No significant differences ($P > 0.05$) were noted in TN of leaves (Figure 2-15 A) among trials (range 10.56 to 13.25 percent dry wt.). Among

petioles (Figure 2-15 B), there were also no significant differences ($P > 0.05$) in TP concentrations from all trials (range 6.23 to 9.33 percent dry wt.).

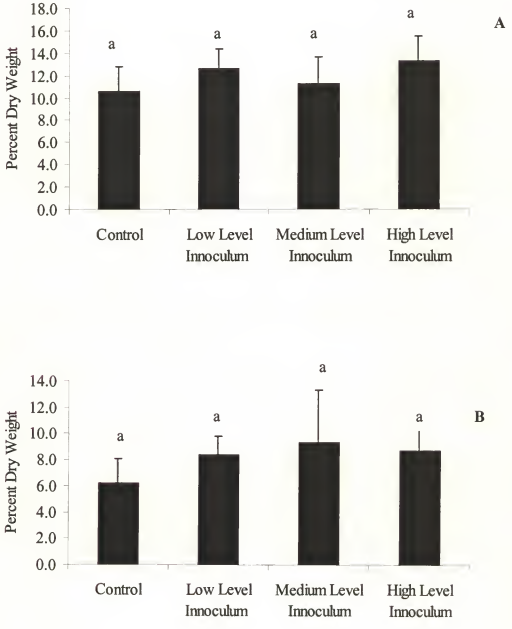


Figure 2-15. TP content in plant parts from semicontrolled experiments. A) Leaves. B) Petioles. C) Rhizomes. D) Roots. Roots. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

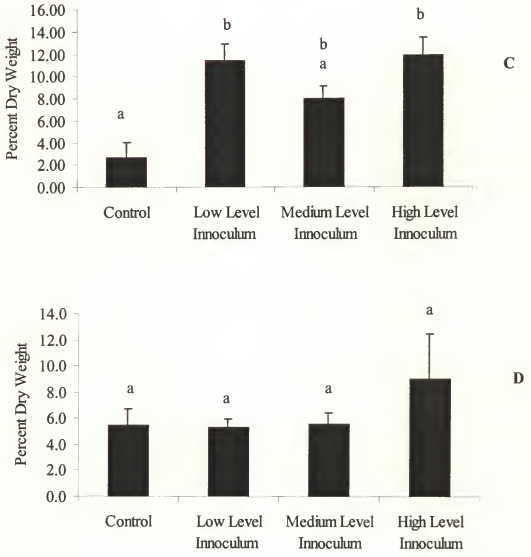


Figure 2-15. Continued.

Two significantly different ($P < 0.05$) homogeneous groups of TP concentrations were identified among rhizomes (Figure 2-15 C). Significantly lower TP was in rhizomes from the control setup (range 1.33 to 4.01 percent dry wt.), while significantly higher concentrations were from the low and high-level treatments (range 5.34 to 9.02 percent dry wt.). Mean concentration of TP in rhizomes from the medium-level treatment (range 4.72 to 6.42 percent dry wt.) was not significantly different from the control setup, and

the low and high-level treatments. Among roots (Figure 2-15 D), no significant differences occurred in mean TP concentrations (range 5.34 to 9.02 percent dry wt.).

Concentration of TN in plant parts from selected bays of Lake Victoria

Data on TN content (per cent dry wt.) in plant parts from selected bays are given in Figure 2-16. There were no significant differences ($P > 0.05$) in TN concentrations of leaves (range 1.41 to 4.07 percent dry wt.) from selected bays of the lake (Figure 2-16 A). Similar trends, with no intersite significant differences ($P > 0.05$), were noted for mean TN concentrations in petioles (Figure 2-16 B, range 1.49 to 3.18 percent dry wt.), and of rhizomes (Figure 2-16 C, range 1.12 to 3.41 percent dry wt.).

Three significantly different ($P < 0.05$) homogeneous groups of mean TN concentrations in roots of water hyacinth from selected bays of Lake Victoria were identified (Figure 2-16 D). Significantly lower TN was in roots from Berkeley Bay and the Kagera River (range 1.13 to 1.67 percent dry wt.), while significantly higher TN was in roots from Fielding Bay (range 5.68 to 7.26 percent dry wt.). Average concentrations of TN in roots from other bays (range 2.11 to 3.59 percent dry wt.) did not significantly differ from the significantly lower (Berkeley Bay and the Kagera River), and the significantly higher (Fielding Bay) concentrations.

Concentration of TP in plant parts from selected bays of Lake Victoria

Average TP concentrations (per cent dry wt.) in water hyacinth parts from selected bays of Lake Victoria are given in Figure 2-17. Among leaves, three significantly different ($P < 0.05$) groups were identified (Figure 2-17 A). Significantly lower concentrations were in leaves from Berkeley, Macdonald, Hannington, Thruston, and Field bays, in addition to sites of Kisinsi-Bule, and the Katonga River (range 0.45 to 3.06

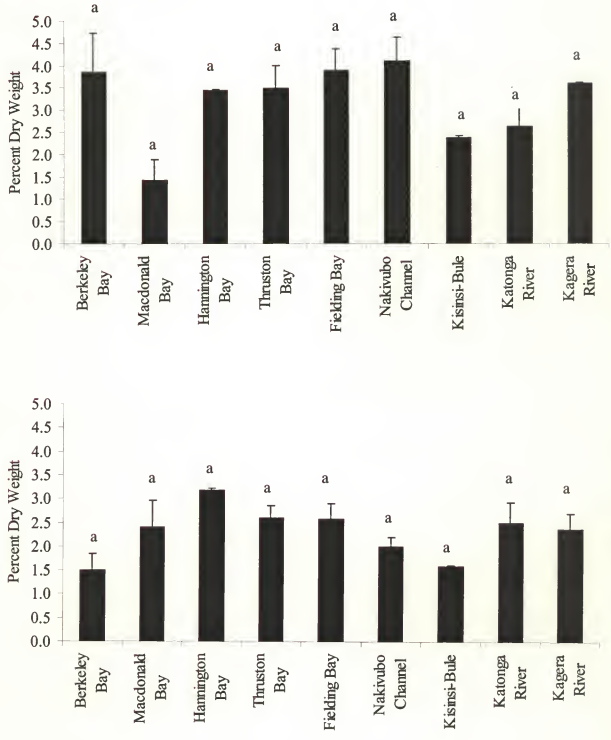


Figure 2-16. TN content in water hyacinth parts from selected bays of Lake Victoria. A) Leaves. B) Petioles. C) Rhizomes. D) Roots. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

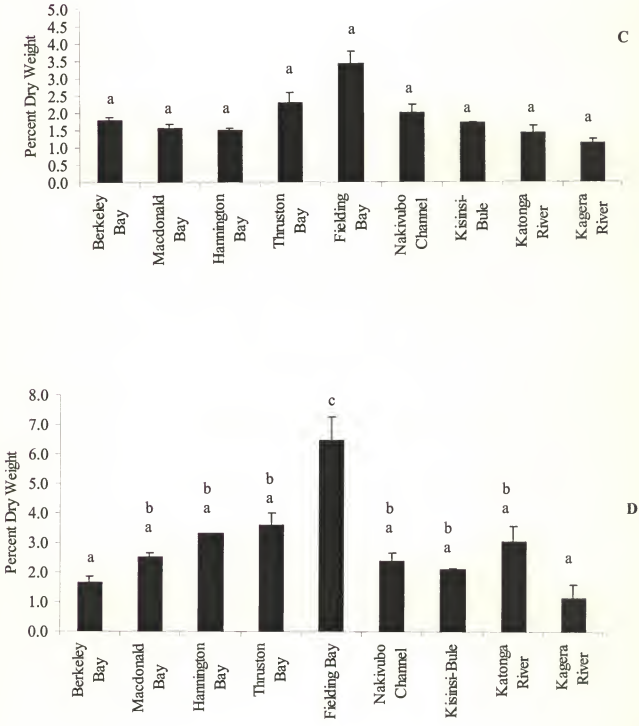


Figure 2-16. Continued.

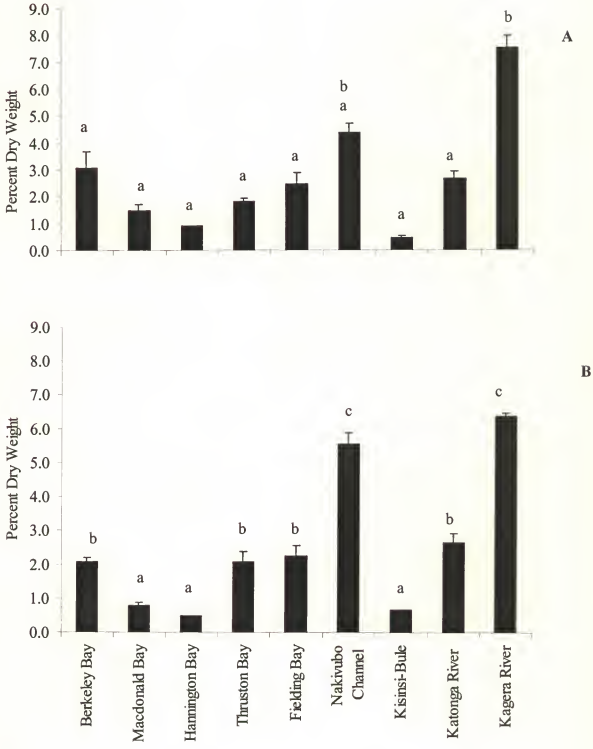


Figure 2-17. TP content in water hyacinth parts from selected bays of Lake Victoria. A) Leaves. B) Petioles. C) Rhizomes. D) Roots. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

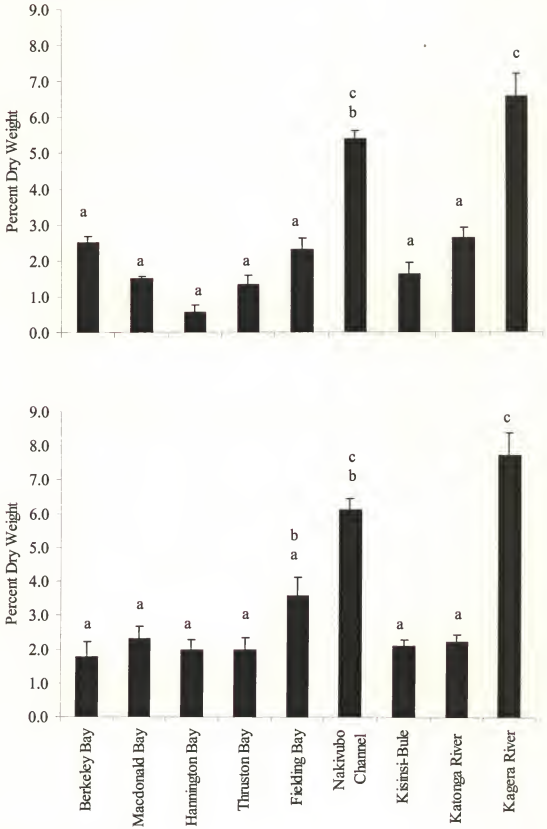


Figure 2-17. Continued.

percent dry wt.). Significantly higher TP was in leaves from the Kagera River (range 7.03 to 7.93 percent dry wt.). Total nitrogen concentration in leaves from the Nakivubo Channel (range 4.03 to 4.71 percent dry wt.) did not significantly differ from the first two groups.

Three groups of mean concentrations of TP in petioles of water hyacinth from selected bays of Lake Victoria were identified (Figure 2-17 B). Significantly lower concentrations of TP were in petioles from Macdonald and Hannington bays, in addition to Kisinsi-Bule (range 0.49 to 0.77 percent dry wt.), while significantly higher concentrations were from the Nakivubo Channel and the Kagera River (range 5.53 to 6.35 percent dry wt.). Concentration of TP in petioles from Berkeley, Thruston, and Fielding bays, in addition to the Katonga River (range 2.07 to 2.66 percent dry wt.) were significantly higher than the former group, but lower than the latter.

Three groups of mean TP (per cent dry wt.) in rhizomes of water hyacinth from selected bays of Lake Victoria were identified (Figure 2-17 C). Significantly lower TP was in rhizomes from Berkeley, Macdonald, Hannington, Thruston, and Fielding bays, in addition to Kisinsi-Bule, and the Katonga River (range 0.58 to 2.61 percent dry wt.), while significantly higher values were from the Kagera River (range 5.92 to 7.18 percent dry wt.). Average TP concentrations in petioles from the Nakivubo Channel (range 5.13 to 5.63 percent dry wt.) were not significantly different from the Kagera River petioles.

Three groups of mean TP (per cent dry wt.) in roots of water hyacinth from selected bays of Lake Victoria were identified (Figure 2-17 D). Significantly lower TP was in roots from Berkeley, Macdonald, Hannington, and Thruston bays, in addition to Kisinsi-Bule, and the Katonga River (range 1.77 to 2.31 percent dry wt.), while

significantly higher values were from the Kagera River (range 7.03 to 8.37 percent dry wt.). Mean concentration of TP in roots from Fielding Bay (range 3.04 to 4.12 percent dry wt.) did not significantly differ from the group with significantly lower TP, while values from the Nakivubo Channel (range 5.78 to 6.44 percent dry wt.) did not significantly differ from either Fielding Bay or the Katonga River.

Total Phosphorus in Sediments from Selected Bays of Lake Victoria

TP concentrations (per cent dry wt.) in sediments from selected bays of Lake Victoria are given in Figure 2-18. Two significantly different ($P < 0.05$) homogeneous

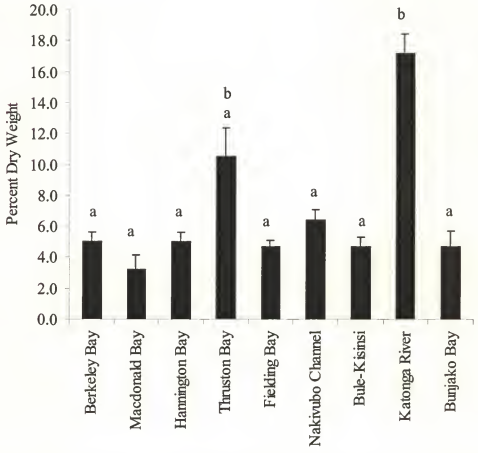


Figure 2-18. Concentration of TP in surface sediments from selected bays of Lake Victoria. Letters above graphs indicate groups that are not significantly different ($P > 0.05$).

groups were identified. Significantly lower TP was in sediments from Berkeley, Macdonald, Hannington, Fielding, and Bunjako bays, in addition to the Nakivubo Channel, and Kisinsi-Bule (range 3.22 to 6.43 percent dry wt.). Significantly higher sediment TP was from the Katonga River inflow (range 15.77 to 18.39 percent dry wt.). Concentration of TP in Thruston Bay sediments (range 9.63 to 12.37 percent dry wt.) was intermediate between the first two groups. In Fielding Bay, inshore sites of Masese, Wanyange, and Kakira (range 3.9 to 7.6 percent dry wt.) had higher TP than the open-water site (2.6 to 2.8 percent dry wt.), but with no significant differences. This was attributed to proximity of inshore sites to the adjacent land from where erosion has a direct influence on sediment P. In the Nakivubo Channel, sediment P increased from the inflow towards the open water (e.g., 4.9 ± 0.5 at 200 m lakeward from inflow, 5.9 ± 1.0 at 400 m lakeward from inflow, and 9.1 ± 0.5 at 600 m lakeward from inflow). This was possibly due to erosion at the inflow and sediment deposition towards the open water. Further out in the open water (i.e., beyond 600 m from inflow), however, sediment P decreased possibly due to dilution as a result of the large volume of lake water. All sites, however, had potentially high levels of sediment P that may trigger growth of algae and water hyacinth if bioavailable.

Discussion

Distribution and Proliferation of Water Hyacinth

Smith (1951) attributed the high growth rate of water hyacinth to its unique biology and ecology including, among other factors, its ability to grow in environments with scarce nutrients, its ability either to grow rooted in sediment or as a free-floating plant on the water surface, and its leaf modification that enables easy distribution with the

slightest wind. Proliferation of water hyacinth on Lake Victoria and other major water bodies in the upper Nile region was so dramatic that within less than a decade, most shores were infested with the plant (Twongo et al. 1991). The conducive growth environment of Lake Victoria was reflected in the ability of water hyacinth to multiply and spread rapidly and exhibit characteristics of luxury plant growth such as greener, broader and longer leaf blades and long petioles. In nutrient-rich habitats such as the Nakivubo Channel, plants were characterized by shorter and fewer roots. Despite low SRP in selected bays, mostly less than 20 $\mu g\ L^{-1}$, water hyacinth proliferation was noted at most sites. This implied that although nutrients are important in plant growth, other environmental factors might also influence plant proliferation. Rapid proliferation of this exotic invasive plant resulted in direct negative socioeconomic influences including interference with navigation (small dugout canoes to translake steamers), fishing, hydropower generation, water abstraction and other activities. In almost every region that it has invaded, water hyacinth has become a nuisance (Davies 1959; Gay and Berry 1959).

The significant negative correlation between SRP and dissolved oxygen indicated the indirect role oxygen plays in water hyacinth growth. Thus, hypoxic to anoxic conditions are likely to enhance water hyacinth growth by making SRP bioavailable through P dissociation from cations such as Fe and Al (Togwell and Schindler 1975; Lovely 1991; Friese et al. 1998). Thus, dissolved oxygen indirectly influenced water hyacinth growth by controlling availability of nutrients, especially SRP. It was assumed that the tropical climate, characterized by an endless growing season, was favorable for plant growth year round especially with regard to temperature. Further, Haller and Sutton

(1973) found that growth of water hyacinth was not affected by pH of 4 to 8, a range commonly found in freshwater bodies including Lake Victoria. They also found that water hyacinths growing in either acid or alkaline water tended to raise or lower pH, respectively, towards neutrality, but this phenomenon not discussed. Interactive effects of these water quality parameters did not limit water hyacinth distribution on Lake Victoria.

Biogeochemical cycles are important in regulating chemical fluxes between surface sediments and the water column (Lovely 1991). Therefore, water depth and electron acceptors such as dissolved oxygen and nitrate-nitrogen are important environmental variables maintaining higher redox potentials. The extensive plant mats imposed a physical barrier to gas exchange between the atmosphere and the water surface thus lowering redox potential by reducing dissolved oxygen in the water. Reduction in redox potential was exacerbated by light limitation of phytoplankton production (Twongo and Balirwa 1996) that can recharge the water column with oxygen. These processes can increase SRP and enhance denitrification leading to loss of N from the system. Increased depth offshore did not correlate with water hyacinth growth and distribution; rather my experiments suggest that exposure to winds and/or waves hinder establishment of water hyacinth mats in such unsheltered habitats.

Nutrients and Growth Characteristics of Water Hyacinth

Occurrence of healthy water hyacinth mats in nutrient-rich habitats such as the Nakivubo Channel in Inner Murchison Bay and Kirinya sewage outflow in Napoleon Gulf stresses the importance of nutrient availability in influencing growth characteristics of water hyacinth. These two sites had a number of features in common (e.g., they were point sources of nutrients, shallow and characterized by persistently low concentrations

of dissolved oxygen that sometimes reached anoxia). Although biological control weevils became established all over Lake Victoria, these nutrient-rich sites remained infested with healthy hyacinth mats.

Low concentration of available N in the water more likely was the major limiting factor to growth of water hyacinth in the Katonga River inflow. Reddy and Tucker (1983) found that N-deficient water hyacinths were characterized by long roots that persisted for more than 1 year, whereas those in N-rich environments had short roots that were replaced more frequently. In addition, Haller and Sutton (1973) found that mass of roots in 0 $\mu g\ L^{-1}$ P nutrient solution was nearly twice that of plants growing in enriched water. Insufficient P apparently stimulated root development of water hyacinths. In my study, field observations showed that either water hyacinth developed dense short roots or very long roots (> 40 cm) in habitats with low concentrations of either N or P or both (e.g., the Katonga River inflow).

The stunted nature of plants at the Katonga River inflow is not clearly understood, but could likely be associated with essential elements and/or N:P ratios that influence growth. Both Sato and Kondo (1981), and Reddy and Tucker (1983) found that water hyacinth grew luxuriantly if N:P ratios were between 2.3 and 5. Only the Kagera River had an N:P ratio (4.6) within this range; the rest of the sites had < 2, suggesting a potential deficiency of available nitrogen. At other sites, N:P ratios were 1.5 at the Sio River inflow, 0.7 in Berkeley, 0.6 in Macdonald, Hannington and Thruston, 0.5 in Fielding, 0.1 in the Nakivubo Channel, 0.9 in Inner Murchison, 0.2 at the Katonga River inflow, and 0.4 in Bunjako Bay. Apparently, no data was available on possible effects of toxins (e.g. phytotoxins) that may retard growth of plants.

Agami and Reddy (1991) studied interspecific relationships between Eichhornia crassipes and Hydrocotyle umbellata L. and found that the root:shoot ratios of E. crassipes in monoculture and mixed stands were similar. Lentz (1999) investigated effects of intraspecific competition and nutrient supply on the bulrush Scirpus ancistrochaetus Scuyler (Cyperaceae) and found that the root:shoot ratio increased with increasing plant density but decreased with increasing nutrient supply. Lentz (1999) also found that plant height and biomass increased with increasing nutrient concentration. In studies of water hyacinth biomass production and phosphorus uptake, Shiralipour et al. (1981 a and b) found that increasing nitrogen concentration lowered the root:shoot ratio. This implied that more shoot biomass was produced at the expense of roots, a phenomenon observed in environments rich in phosphorus such as the Nakivubo Channel of Inner Murchison Bay.

Extensive root biomass would present a large surface area for nutrient absorption. Roots of plants grown in phosphorus enriched trials exhibited a grey to black coloration, but those in P-deficient tanks showed iridescent blue-purple color. Such root variance might be used as an indicator of the nutrient status of the environment. Although field observations showed an inverse relation between root length and nutrient availability, plants grown under semicontrolled conditions did not reveal this trend probably due to its short duration.

Water hyacinth biometrics data from selected bays of Lake Victoria showed that sites with high SRP concentrations in the water ($> 20\ \mu g\ L^{-1}$) (e.g., the Nakivubo Channel) had significantly longer and broader leaf blades, and longer petioles. Those sites with low concentrations of SRP ($< 20\ \mu g\ L^{-1}$ e.g., most bays) had significantly

shorter and slender leaf blades, and shorter petioles. However, under semicontrolled laboratory condition, lack of significant differences in leaf blade length and width, and petiole length among most treatments contradicts field data. This could however, be attributed to the short time exposure of the semicontrolled experiments, and the small size of tanks that were used, resulting in crowding of plants within a short time (< 2 months).

Significant positive correlations between water hyacinth biometrics data (length of leaves, petioles and roots, and width of leaves), and nutrients (NO_3-N and SRP) in field enclosure experiments suggested the importance of these nutrients in influencing growth characteristics (biometrics data) of this plant. However, under semicontrolled laboratory conditions, correlation was significant only between NO_3-N and root length in Experiment 1, and leaf blade length and width in the low-level treatment, and with petiole length in the high-level treatment of Experiment 2. Further, correlation with SRP was significant only with leaf width in the low-level treatment, and with petiole length in the high-level treatment. Lack of significant correlations in most trials under semicontrolled conditions as opposed to field enclosure experiments, was probably a limited time exposure in the former, especially as a result of limited space in experimental tanks, leading to crowding in a short time.

Root length under semicontrolled experiments was not easily determined since both old and new roots were on the same plants. It would have been better if all old roots had been trimmed so that monitoring root development was easy, but this approach would have altered plant development and would have required time for development of new roots before taking data on root length.

Lack of significant regressions between concentration of nutrients (NO_3-N and SRP) in the water and most growth parameters (specific and relative rates of increase in numbers of ramets and leaves, in addition to wet mass) assessed in field enclosure experiments, is difficult to explain despite the luxuriant growth of the plants at nutrient-rich than at nutrient-poor sites. It is probable that the short time it took for plants to multiply and fill the enclosures, leading to crowding, may have masked differences among sites with different ambient nutrient concentrations. Regression among most trials under semicontrolled experiments were also not significant, except between NO_3-N and specific rate of ramet increase (in the low-level trial of Experiment 1), and SRP with relative growth rate (in low-level treatment of Experiment 1, in addition to the medium and high-level treatments of Experiment 2). This implied that nutrients (NO_3-N and SRP) could not easily be used to predict growth (SGR, RGR, and recruitment of ramets and leaves) other than biometrics characteristics of the plant.

In streams and rivers, nutrients are transported downstream through a phenomenon termed nutrient spiraling, whereby nutrient elements are taken up by organisms and released back into the environment (i.e., a spiral distance) (Maltchik et al. 1994; Pringle et al. 1988; Newbold et al. 1981). In lotic habitats where biological productivity is high, a spiral distance is expected to be short because of high elemental uptake rates (Newbold et al. 1981). Occurrence of water hyacinth in streams forms patches that reduce spiral distances, especially for nitrogen and phosphorus. It is possible that low but stable concentrations of nutrients in the Kagera River sustained water hyacinth through nutrient spiraling and could be a major factor accounting for luxuriant growth of this plant.

Luxuriant growth of water hyacinths along the shores of the Kagera River may also be partly due to failure of establishment of biological-control weevils.

Elsewhere in Lake Victoria, water hyacinth initially exhibited rapid proliferation, but depletion of nutrients in the water column during peak biomass cover, coupled with grazing by biological-control weevils, resulted in suppressed growth (NARO 2002). This was followed by sinking of extensive mats of water hyacinth that had sequestered nutrients, which were released into the water column during decay.

In this study, water hyacinth grew well in all treatments except the control in which plants were stunted. Significantly lower concentrations of NO_3-N and SRP for Experiments 1and 2 formed the starting point for determining the lowest concentrations of these nutrients in influencing water hyacinth growth characteristics and biomass accumulation. However, lack of significant differences among all treatments, other than the control, in relation to SGR, RGR, overall mean wet mass, doubling time, and specific and relative rates of ramet recruitment seemed to suggest that nutrient concentrations in and above the low-level treatment were favorable for hyacinth growth. In addition, the significantly higher doubling time, and the significantly lower relative leaf recruitment in the control setup of both experiments, in addition to the significantly lower RGR in Experiment 2, suggested suppressed growth at concentrations of NO_3-N and SRP in the control setup. Deficiency in these macronutrients resulted in very slow or arrested growth as was noted in the control setup. In nutrient-enriched water, plants grew rapidly, and dark green foliage was likely indicative of a favorable nutrient environment. Thus, it is likely that concentrations of NO_3-N and SRP between values in the low-level treatment of Experiment 2 (i.e., 175.9 ± 26.5 μg L^{-1} NO_3-N and 44.5 ± 2.8 μg L^{-1}SRP), and the

control tanks (121.7 ± 9.9 μg L^{-1} NO_3-N and 34.2 ± 1.8 μg L^{-1} SRP), could sustain water hyacinth in Lake Victoria. It was on this basis that concentrations at or below 121.7 ± 9.9 μg L^{-1} NO_3-N and 34.2 ± 1.8 μg L^{-1} SRP were considered limiting to water hyacinth growth.

Water hyacinths can persist for almost 1 year in water devoid of plant nutrients (DeBusk and Dierberg 1989), suggesting that this species efficiently conserves nutrients either via a slow rate of detritus production or efficient translocation of nutrients from senescing to growing tissue. Petr (1992) reported that water hyacinth and Salvinia molesta can undergo explosive growth in clean waters implying that these plants can grow even in very poor nutrient environments. During my study, water hyacinths in the control tanks persisted throughout the experiment, though with signs of nutrient deficiency (including chlorosis of leaves). Survival of these plants was possibly due to utilization of nutrient reserves accumulated in tissues before initiation of the experiment.

Scheffield (1967) reported that reduction of SRP to 20 μg L^{-1} in natural waters suppressed proliferation of algae and aquatic macrophytes. Reddy et al. (1989) noted that growth of hyacinth increased until N and P concentrations reached 5,500 μg L^{-1} and 1,060 μg L^{-1}, respectively. The differences between minimum concentrations of N and P in the current study and the above concentrations (5,500 μg L^{-1} NO_3-N and 1,060 μg L^{-1}SRP) are indicative of the ability of hyacinth to grow under a wide range of nutrient concentrations. The mean value of 121.7 ± 1.8 μg L^{-1} NO_3-N and 34.2 ± 1.8 μg L^{-1} SRP in the control setup in the current study could limit water hyacinth growth in natural waters, bearing in mind the intricacy of competition from other organisms (e.g., algae, bacteria, and other macrophytes) for this nutrient. In addition, the various biogeochemical

transformations could lead to shifts in SRP concentration from this mean value, thus influencing water hyacinth growth.

Ratios of N:P in all trials of semicontrolled experiments were considered favorable for water hyacinth growth since most were in the range (2.3 to 5.0) considered optimum for plant growth and production (Sato and Kondo 1981; Reddy and Tucker 1983). Slightly higher ratios (N:P > 5.0) were found in all treatments of Experiment 1 (5.2 in low, 5.9 in medium, and 5.5 in high-level treatments) and indicated slightly excess N, but were close to the optimal range. In spite of optimal N:P ratios, low concentrations of N and P in the control setup suppressed growth of water hyacinths. In Lake Victoria, most bays sampled had N:P ratios below the optimum range (2.3 to 5.0), except in the Kagera River waters (4.6). Low N:P ratios possibly indicated potential N-limitation. Previous studies indicated N to be the limiting nutrient for phytoplankton production in Lake Victoria (Talling and Talling 1965; Mugidde 1993; Lehman and Bronstrator 1993). It is, however, not known whether their findings can be extrapolated to macrophyte production. However, tissue concentrations of TN (> 1.3 % dry wt.), and TP (> 0.13 % dry wt.), considered the thresholds for most aquatic angiosperms, were indicative of non limiting N and P to plant growth (Gerloff and Krombholz 1966) in Lake Victoria.

In both nutrient-enriched tanks and field experiments at nutrient-rich sites, crowding from vegetative propagation limited horizontal expansion, and plants resorted to vertical expansion. This was considered an adaptive response to mitigate adverse effects of crowding. For example, development of nonbulbous long petioles enhances a plant's ability to capture light when crowding leads to a closed canopy (Center and Van 1989). Reduction in ramet production was also considered an adaptive response to invest

resources in already existing plants rather than in production of ramets where competition for resources (e.g., space, light, and nutrients) was already limiting. As crowding intensified and vegetative propagation was suppressed (through reduced ramet production), flowering increased. Geber et al. (1992) made similar observations when studying genetic differences in the clonal demography of water hyacinth. This was also considered a survival strategy for future generations as seeds. For semicontrolled experiments, when crowding occurred, the experiments were terminated, as I wished to eliminate data influenced by another external factor (crowding). Although not quantified in semicontrolled experiments, the fairly green color in the nutrient-enriched tanks was indicative of high algal biomass in the early weeks of the experiment. This color, however, disappeared with time due to light limitation as hyacinths in all treatments covered most of the surface.

Field experiments on growth of water hyacinth showed similar growth characteristics, with plants initially exhibiting horizontal expansion but reverting to vertical growth when crowded. The shift from horizontal to vertical growth was characterized by a shift in leaf form from bulbous to nonbulbous. Plants then grew tall and slender, and vegetative propagation decreased.

Studies on growth characteristics of water hyacinth have shown that both light quantity and quality influence leaf plasticity (Smith 1981; Vince-Prue and Tucker 1983). The amount of light reaching the shoot apex varies between the edge and center of a water hyacinth mat (Penfound and Earle 1948; Knipling et al. 1970). In addition, Richards and Lee (1986) found that the major effects of light on water hyacinth leaf-form were produced by a reduced red:far red (R:FR) ratio. They reasoned that a decrease in

R:FR has two effects i) reduced petiole swelling, and ii) increase in leaf length. Thus, it was concluded that spectral quality and not light quantity is the major factor controlling petiole inflation and that a reduction in R:FR ratio stimulates petiole elongation. Furthermore, Methy and Roy (1993) noted that low R:FR ratio resulted in a pronounced decrease in the root:shoot ratio and generally led to larger leaf blades. During field investigations in Lake Victoria, the inflow of the Katonga River had the highest population of bulbous growth forms (inflated petioles), with the longest roots, while elsewhere, this leaf form dominated only the outer fringes of hyacinth mats. In addition, luxuriant hyacinths characterized by long, uninflated petioles, large leaf blades and short roots dominated the Nakivubo Channel and the Kirinya sewage outflow. Hyacinths at these two sites remained crowded most of the year, possibly leading to reduced R:FR, while at the Katonga River inflow, plants were relatively dispersed with high R:FR. Although the light climate was not assessed during this study, field observations are in agreement with previous studies (e.g., Methy and Roy 1993; Richards and Lee 1986) on water hyacinth leaf-form plasticity and root characteristics. Additional studies are recommended on hyacinths of the Katonga River inflow.

There was a significant ($P = 0.05$) inverse correlation ($r = -0.625$) between SRP and dissolved oxygen in the water. High SRP concentrations in the Nakivubo Channel and probably at the Kirinya sewage outflow, where dissolved oxygen concentrations were mostly < 1 mg L^{-1} for most of the year, were likely the major factor promoting the huge water hyacinth biomass at these sites year round. The Nakivubo Channel and adjacent habitats in Inner Murchison Bay were considered the most serious plant management areas because water hyacinth showed the highest rate of biomass buildup, rates of ramet

increase, relative growth rate (RGR), and specific growth rate (SGR) in the field enclosures over time. Lack of statistically significant differences in these parameters among sites was possibly a result of crowding that occurred in a shorter time among enclosures in the Nakivubo Channel, and remained in this state over the entire sampling period. In Thruston Bay, highest values for similar biometrics data were recorded at Kafunda, whose nutrient levels (N and P) were not significantly different ($P > 0.05$) from Nkombe. This was more likely associated with shelter from wind than nutrients.

Tissue Nutrient Accumulation and Ambient Nutrients

Gerloff and Krombholz (1966) found that when growth requirements (other than nutrients) were adequate, tissue concentrations below a critical level were associated with deficiencies of that element in the environment, resulting in reduced yields. Tissue contents above a critical concentration had no effect on yields and were indicative of luxury consumption. They also found that critical tissue N and P concentrations for most aquatic angiosperms were approximately 1.3 % and 0.13 % of plant dry weight, respectively. Gerloff and Krombholz (1966) also found that average values of N and P for most aquatic plants correlated well with water concentrations of these nutrients. In the current semicontrolled experiments, TN was only above the critical level (> 1.3 % dry wt.) in leaves and rhizomes from the high-level treatment, and petioles from the medium-level treatment, while tissue TP was above critical level (> 0.13 %) in plants from all treatments and the control. Tissue TP above 0.13 % of dry weight in plants from control tanks probably indicated that water hyacinths can conserve nutrients, or exhibit luxury consumption even when growing in nutrient-poor environments.

DeBusk and Dierberg (1989) found that bioavailable N and P in the environment influenced tissue concentrations. They found that high nutrient loading resulted in approximately 2.0 % N, while low loading led to about 1.0 % N in hyacinth tissues, with roots having the highest content. However, the current study did not find a direct relationship between ambient and tissue N and P. Data from the current study contradict findings by Gerloff and Krombholz (1966) that elemental content in tissues was an indicator of element availability in the environment. For example, one would expect highest tissue TN in plants from sites with significantly higher NO_3-N (e.g., Sio River inflow in Berkeley Bay, and the Kagera River), but this was not the case. Thus, tissue TN did not reflect ambient concentration of NO_3-N. However, since tissue concentrations were above the critical level (> 1.3 per cent dry wt) (Gerloff and Krombholz 1966), it could imply that nitrogen was not limiting water-hyacinth growth in Lake Victoria.

Plants from the Kagera River had the highest TP concentration in their tissues despite significantly lower SRP (17.2 ± 1.8) in the water. This was possibly a result of constant replenishment of nutrients through stream loading (Newbold et al. 1981). Plants from the Nakivubo Channel were among those that sequestered the most P, and there was a decreasing trend along the channel flow toward the open lake probably due to dilution of nutrients and possible binding of P to oxidized cations such as Fe^{3+} (Togwell and Schindler 1975; Lovely 1991; Friese et al. 1998) in the water. Plants from within and outside experimental enclosures showed similar tissue P concentrations hence enclosing the plants did not have negative effects on growth.

Mean concentrations of TP in tissues of plants cultured under semicontrolled conditions did not directly correlate with SRP concentrations in experimental tanks. The

above-water biomass (leaves and petioles) were the main storage parts for both N and P. Gerloff and Krombholz (1966) found that tissue TP content of > 0.13 per cent dry wt. indicated nonlimiting P in the environment. Since data for the current study showed P content of > 0.13 per cent dry wt. in both field enclosures and semicontrolled experiments, it is possible that P was not limiting water hyacinth growth in Lake Victoria. Plants also could have exhibited luxury nutrient uptake, or conserved nutrients in excess of their requirements.

Studies on nutrient accumulation by water hyacinth as a function of the growth environment have yielded conflicting results. Boyd and Vickers (1971) reported no correlation between nutrient status of the growth environment and tissue N and P levels. On the other hand, Moorhead et al. (1988) reported increased tissue N with increased nutrient availability. The current study found no direct relation between tissue and environmental concentrations of N and P. This demonstrated the complexity of the environment in which plants grow and indicated interactions of an array of environmental factors during plant growth. For example, Ower et al. (1981) reported inhibition of N uptake by either increasing P or decreasing N in the water, and that increasing P above 0 $\mu g\ L^{-1}$ inhibited accumulation of N. Phosphorus uptake was stimulated by elevation of N or P or both. Accumulation of P was enhanced by increasing P concentration but was reduced with increasing N concentrations. The current study and others have shown that high tissue P concentration (> 0.13 % dry wt. considered the critical level by Gerloff and Krombholz 1966) indicated that water hyacinth was an important sink for nutrients, and if harvested before senescence, could lead to cleaning the lake by removing some of the nutrients from the water. However, if left to decompose within a system, decomposing

hyacinths (as will be elaborated in Chapter 4) become a significant nutrient source for either nuisance algal blooms or further proliferation of water hyacinths.

Overall, TN and TP concentrations in plant parts were not proportionately related in most cases to nutrient concentration in experimental tanks or in the lake. Leaves were the main storage units for nutrients, but as water in experimental tanks became richer in nutrients, there were minimal differences in nutrients sequestered in different plant components.

Minimum Ambient Nutrients for Water Hyacinth Growth

Several studies have assessed the concentrations of N and P that trigger maximum water hyacinth growth and production (e.g., Desougi 1984; Haller and Sutton 1973). However, my study investigated the lowest N and P concentrations that could limit production of hyacinth plants. Desougi (1984) studied nutrient demands of water hyacinth in the White Nile, Sudan, and found maximum growth at 21,000 $\mu g\ L^{-1}$ N. Growth of water hyacinth also increased with increasing phosphorus. I found that the rate of P increase in the water was not proportional to an increase in growth parameters (SGR, RGR, and specific and relative rates of leaf and ramet recruitment), and that N and P were the limiting factors for growth and reproduction. Phosphorus concentrations as high as 60,000 $\mu g\ L^{-1}$ were not associated with increased growth and were not toxic to water hyacinth (Desougi, 1984). In a related study, Haller and Sutton (1973) found maximum growth of water hyacinth at 20,000 $\mu g\ L^{-1}$ P and that toxicity began at 40,000 $\mu g\ L^{-1}$. Haller et al. (1970) found that 100 $\mu g\ L^{-1}$ SRP was the critical concentration of P for maximum growth of water hyacinth. My study found that concentrations of 176 $\mu g\ L^{-1}$

NO_3-N and 45 μg L^{-1} SRP were the lower limit for healthy hyacinth growth, while concentrations of ≤ 122 μg L^{-1} NO_3-N and ≤ 34 μg L^{-1} SRP resulted in arrested growth.

The very low N:P ratios at the Katonga River inflow were indicative of N deficiency. However, tissue TN concentrations were above the critical level (1.3 %), likely indicating efficient conservation of the scarce N. This and data from semicontrolled experiments contradict the findings of DeBusk and Dierberg (1989) that the concentration of available nutrients proportionately influences tissue nutrient concentration. I found only tissue P far above the critical (0.13 %), agreeing with DeBusk and Dierberg (1989) that this indicated luxury consumption of P. The high levels of ambient P could have limited, or even suppressed N absorption by water hyacinth, leading to stunted plants. Although other plants such as Cyperus papyrus L. were not examined, visual observations showed poor health compared to those in Murchison Bay where N and P were in ample concentrations.

Shiralpour et al. (1981a and 1981b) found that P uptake was influenced by N concentrations, and that maximum P uptake occurred at 5,000 μg L^{-1} when N was 10,000 μg L^{-1}. When P concentrations in the water were high, the amount of P absorbed by plants was lower than when P concentrations were lower (Shiralpour et al. 1981a; Haller et al. 1970). Low concentrations of N in the Katonga River inflow was probably one of the causes for the stunted growth of water hyacinth. The low concentration of N probably limited P uptake, as well as rendering available N below the critical level for water hyacinths. Plants at this site adapted to these conditions by developing high root:shoot ratios to increase the absorptive surface area of roots for the limited N.

Increasing availability of N may trigger luxuriant growth of water hyacinths in the Katonga River inflow. However, since the goal of environmental managers is to control proliferation of this plant, the observations were welcomed. Stunted growth of water hyacinth in the Katonga River may partially be explained by Fe deficiency, as plants were chlorotic (Morgan 1954). However, this was not assessed during this study, hence further studies are recommended in this direction.

Human Activities in the Lake Victoria Catchments

The human population of the Lake Victoria basin is not only high (> 100 persons km^{-2}), estimated at more than 27 million (Ntiba et al. 2001), but has one of the highest rates of increase (averaging 3.5 % per annum during the period 1970 to 1980) in the world (Cohen et al. 1996). Human activities within the catchments have increased production of sewage, land clearance and fertilizer use for agricultural production, resulting in increased cultural loading of nutrients to the lake (Bootsma and Hecky 1993). Unless human activities are rationally monitored and regulated, the health of Lake Victoria will continue to deteriorate with one likely biological expression of proliferation of aquatic macrophytes such as water hyacinth. Sections of the lake with major point-source nutrient inputs such as the Nakivubo Channel in Murchison Bay and the Kirinya Stream in Napoleon Gulf, Uganda, both of which receive sewage discharges, display luxuriant water hyacinth mats despite establishment of the biological-control weevils. Increased P concentrations in Lake Victoria (Lehman and Bronstrator 1994) are partly attributed to these point sources, but diffuse sources increasingly are becoming important (e.g., high P concentrations recorded during this study along the shore at Kakira, a site in Fielding Bay, were likely due to run off from sugar cane plantations).

Inshore (littoral) zones of the lake have high concentrations of nutrients (Hecky 1993), hence problems with aquatic plants are likely to be more severe there if management measures do not address the overall eutrophication problem.

Conclusions

Lack of significant intersite differences in NO_3-N concentration in the water from selected bays possibly indicated that nitrogen similarly influenced water hyacinth growth in most bays. Available literature information indicated that phytoplankton primary production was nitrogen limited (e.g., Lehman and Bronstrator 1993; Mugidde 1993). If this scenario also applies to macrophytes (including water hyacinth), then nitrogen may be one of the critical factors to consider in management of water hyacinth by applying the "Law of the minimum". However, high concentrations of N in most plant tissues were above the threshold (i.e., > 1.3 % dry wt.) (Gerloff and Krombholz 1966), possibly indicating no nitrogen limitation in water hyacinth growth. Tissue P was also above threshold (0.13 % dry wt.) values in plant tissues from all sites, which possibly indicated that P was not limiting plant growth (Gerloff and Krombholz 1966) in Lake Victoria. In both cases, it also could imply luxury nutrient uptake, or efficient conservation of nutrients in tissues. This calls for a holistic approach in addressing the problem of nutrient loading, while directing more efforts to point sources.

Point-source nutrient inflows were the most important zones where water hyacinth became a permanent problem (Murchison Bay in general and the Nakivubo Channel in particular) in Lake Victoria, and made this bay the most important hot spot for water-hyacinth proliferation and/or resurgence. Other important hot spots were Bunjako Bay and Kirinya sewage outflow in Napoleon Gulf near Jinja. Long-term management

strategies should monitor water quality at these point sources during development of appropriate recommendations and policies for management. Non-point sources (e.g., sugar cane plantations of Kakira) need to be monitored and managed in order to reduce nutrient loading to the system. Efficient control measures for aquatic plants and reduction of nutrient loading should be part of any strategy to manage aquatic plants, water quality and fisheries.

Phosphorus loading at sites displaying significantly higher SRP in the water, notably, the Nakivubo Channel (240.1 ± 12.0 μg L^{-1}), the Katonga River (91.0 ± 4.1 μg L^{-1}), and the Sio River (42.6 ± 4.6 μg L^{-1}), and possibly at the Kirinya Stream outflow, need to be given urgent attention aimed at reducing nutrient loading. Phosphorus loading through the Sio River may not be a serious problem since significantly higher P levels were localized at only its confluence with the lake. However, addressing the problem for long term management is recommended.

Ambient nutrient concentrations in excess of 45 μg L^{-1} SRP and 176 μg L^{-1} NO_3-N led to luxuriant growth of water hyacinth. Management measures aimed at controlling water hyacinth through a bottom-up approach (nutrient management) should focus on reducing N and P loading to a level where ambient SRP and NO_3-N are below 34 μg L^{-1} and 122 μg L^{-1}, respectively.

Water hyacinth grows luxuriantly in nutrient-rich environments. Longer and broader leaf blades, longer nonbulbous petioles, and shorter sparse roots characterized luxuriant growth of this plant. It is therefore possible to use water hyacinth as a biological indicator of the nutrient status of a given environment.

CHAPTER 3
PHOSPHORUS RELEASE FROM SURFACE SEDIMENTS INTO THE WATER COLUMN

Introduction

Lake sediments can be an important phosphorus source (Holdren and Armstrong 1980) for promoting aquatic plant growth and sustaining and/or accelerating eutrophic conditions (Wildung et al. 1974; Bates and Neafus 1980). They may also act as a phosphate buffer to maintain constant P concentrations in the overlying water (Pomeroy et al. 1965) through gradual release. Frink (1967) indicated that sediments in a Connecticut lake could act as a nutrient reservoir capable of supporting plant growth indefinitely without allochthonous inputs.

Many lentic systems can remain eutrophic for long periods even though external nutrient sources are eliminated (Jeppsen et al. 1991; Schadlow and Hamilton 1995; Hu et al. 2001). Delay or even failure of lentic ecosystems to show increased water quality after reduction of external P loading is due to continued P release from sediments (Ahlgren 1977; Larsen et al. 1981; Ryding 1985; Welch et al. 1986). Further, inorganic and organic nutrients are continuously sedimented on the lake bottom, but due to various biological, physical, chemical and mechanical processes, they can be returned to overlying water (Forsberg 1989).

Release of nutrients, especially orthophosphates and ammonia-nitrogen, from sediments can be significant. Thus, although the external nutrient loading may be reduced, nutrients can gradually be released back into the water column from

contaminated sediments and may delay improvement in water quality and cause attendant problems including proliferation or resurgence of aquatic macrophytes. Reddy and Gale (1994) found that reduction in external nutrient loading may not result in significant changes in lake trophic status, since nutrient diffusion and sediment resuspension can potentially supply most of the necessary nutrient requirements to the water column.

Increased nutrient loading has led to culturally induced eutrophication of lakes globally (Andersen 1982) as currently seen in Lake Victoria (Hecky and Bugenyi 1992; Lung'ayia and Kenyanya 2002) and is characterized by increased primary production of phytoplankton, periphyton, and/or macrophytes (Pinto-Coelho and Barcelos 1999). Most eutrophication models are based mostly on the role of allochthonous nutrient inputs and often ignore internal nutrient loading (Pinto-Coelho and Barcelos 1999) as an important source of nutrient loading. Nutrient release from bottom sediments through resuspension, bioturbation, or diffusion may play an important role in determining the trophic state of an aquatic ecosystem (Barbanti et al. 1992; Reddy and Gale 1994). Internal P loading can contribute significantly to the overlying waters at levels comparable to external loading (Serruya et al. 1974; Ravera 1983; Premazzi and Provini 1985).

In Lake Victoria, management measures ought to address the influence of landuse activities (Ntiba et al. 2001) that have direct or indirect influences on the structure and function of the lake. Catchment activities (especially agriculture and urbanization) are increasingly drawing local, regional and international attention regarding their effect on water quality. Water hyacinths (Twongo 1996; Twongo and Balirwa 1996) and algal blooms (Mugidde 1993) have been increasing in Lake Victoria. Water hyacinths have proliferated mostly in shallow littoral zones of the lake; it is here that exchange of

nutrients between sediments and the water column is of utmost importance (Ryding and Forsberg 1977) in sustaining the plants.

The physical and chemical characteristics of sediments and their adsorption and desorption properties are among the data sets necessary for understanding phosphorus exchange processes between sediments and the overlying water (Bostrom and Petterson 1982). In his pioneering studies on chemical fluxes between surface sediments and the water column, Mortimer (1941 and 1942) demonstrated immobilization of P in oxic sediments by sorption with Fe^{3+} and, under reducing conditions, that P was mobilized by reduction of Fe^{3+} to Fe^{2+}. Phosphate equilibrium between surface sediments and the water column is regulated by the redox potential of the sediment-water interface (Stumm and Morgan 1970).

High concentrations of oxidized nitrogen (i.e., NO_2-N and NO_3-N) in the water may increase phosphorus binding in the sediment by stabilizing redox potential at a high level in both the water column and surface sediments (Andersen 1982). Lakes displaying summer stratification and anoxic hypolimnia release significant amounts of phosphate from profundal sediments where low concentrations of oxidized nitrogen ($< 100\ \mu g\ L^{-1}$) occurred. In contrast, no release occurred where oxidized nitrogen (especially NO_3-N) in the anoxic hypolimnion exceeded $1{,}000\ \mu g\ L^{-1}$.

Others have demonstrated exchange of P between sediments and overlying water both in the presence and absence of oxygen (e.g., Olsen 1958 and 1964). However, the rate of P release from anoxic sediments can be several orders of magnitude higher than under oxic conditions (e.g., Hays and Philips 1958; Fillos and Swanson 1975).

Phosphorus is usually the limiting nutrient controlling aquatic plant productivity in temperate aquatic systems (Pinto-Coelho and Barcelos 1999), but nitrogen limits primary production in Lake Victoria (Talling and Talling 1965; Mugidde 1993; Lehman and Bronstrator 1993). In the tropics in general and in Africa in particular, the role of sediments as a nutrient source is poorly known, although Andersen (1982) reaffirmed the importance of N as the nutrient limiting primary production in the tropics.

Lake and river sediments may act as sources or sinks for a variety of solutes including nutrients (Woodruff et al. 1999). During stratification, large amounts of phosphorus accumulate in anoxic hypolimnia of lakes due to release of P from underlying sediments (Caraco et al. 1993; Kleenberg et al. 2001; Krivtsov et al. 2001), coupled with plankton rain from the epilimnion (Lewis and Syvitski 1983; Ripl 1993; Silver et al. 1998). Chiaro and Burke (1980) found that exchange of total dissolved phosphorus was unrelated to nutrients within the sediments or overlying water but was related to oxygen depletion. This is consistent with the widely accepted view that phosphorus exchange is controlled principally by redox reactions involving major cations such as Fe, Al, or Mn or all three (Lovely 1991). However, Kim et al. (1997) and Woodruff et al. (1999) found that the composition of water overlying the sediments was important in controlling nutrients and influenced fluxes at the sediment-water interface.

During the water-hyacinth biomass peak and collapse of late 1998 in Lake Victoria (NARO 2002), it was expected, though not assessed, that the sunken water hyacinth contributed immensely to both the amount of nutrients (phosphorus) and changes in sediment characteristics. Such changes may have altered the rate and amount of nutrient release from surface sediments. It was therefore inferred that phosphorus transfer to the

sediments occurred mainly through deposition of water hyacinth debris (Bostrom 1988) at the time of sinking. The decomposed hyacinths may have released phosphorus into the water column, a process that was not investigated. Phosphorus release can be minimal from living macrophytes but considerable during macrophyte dieback (Forsberg 1989), a phenomenon similar to the extensive demise of water hyacinth during the unprecedented sinking. If sufficient phosphorus and other nutrients were released from hyacinth-derived sediments, then with perfect recycling, the system could be self-sustaining in supporting resurgence of water hyacinth if proper water-hyacinth control measures are not in place.

Quantifying internal phosphorus loading involves assessing inputs, outputs and phosphorus present in the water column as a function of time. This would enable determination of net P fluxes between sediments and the water column (Lee et al. 1976). This approach is time-consuming, costly and often not feasible given the difficulties of identifying and monitoring nutrient sources (e.g., rivers, streams, atmospheric wet and dry deposition, land runoff, etc.) of aquatic systems (Premazzi and Provoni 1985).

Serruya et al. (1974) suggested that nutrient regeneration is a two-way process initially involving bacterial activity and physicochemical reactions that determine nutrient concentrations in pore water, followed by release across the sediment-water interface. Extensive mats of water hyacinth continuously covered Thruston Bay between 1991 and 1998, while mobile mats occasionally covered Fielding Bay for periods of less than a week. The two bays were selected in this study because of differential water hyacinth cover due mainly to shelter from offshore winds. Thus, Thruston Bay is a well sheltered bay, with shallow littoral zones having organic sediments that were thought to be rich in nutrients; these features are thought to have partly contributed to accumulation

of hyacinth biomass. Fielding Bay, on the other hand, is an open bay (not sheltered), and has mostly sandy sediments, features that do not enhance water hyacinth establishment. Fielding Bay, where there was only occasional water hyacinth cover, was used as the reference bay for this study. Sinking of extensive mats of water hyacinth occurred in late 1998 and is thought to have had drastic effects on sediment characteristics including carbon content. This could have altered P release rates into the water column.

The objective of this study was to assess the rate of phosphorus release under hypoxic and well-oxygenated conditions, from surface sediments assumed to be derived from sunken and decomposed hyacinth, to the water column. Sediments examined were from two bays (Thruston and Fielding) differentially infested by water hyacinth.

Materials and Methods

Field sampling

Phosphorus exchange at the sediment-water interface was estimated via incubation of intact sediment cores in the laboratory (Bonetto et al. 1994; Kleenberg et al. 2001). Sediment cores were taken using a piston corer to which metal rings (≅ 5 kg) were attached to provide the necessary weight to sink the corer into the sediment. The corer was equipped with a trigger which, when operated, started the coring operation. The corer was then retrieved to just below the water surface, a tightly fitting rubber stopper plugged at the bottom of the tube to prevent sediment loss before removing the corer from the water. This procedure minimized disturbance at the sediment-water interface during sampling. Core tubes were Plexiglas (Rochester, New York, USA) (83 cm long x 6.7 cm internal diameter). Length of cores varied depending on sediment type (e.g., in Thruston Bay with flocculent sediments, cores of 20 cm were collected, while in Fielding Bay with

mostly sandy sediments, cores of 10 cm were collected). It was unnecessary to collect longer cores since only the top 0 to 5 cm was required for the experiment. Sediment cores were taken in triplicates from each of Thruston and Fielding bays for each of Experiments 1 and 2. Selection of bays for taking cores was based on prior information of water hyacinth infestation.

The sediment cores were transported intact to the FIRRI laboratory and left upright for 2 to 3 h. Overlying water was decanted slowly by pushing a rubber stopper upwards from the bottom of each tube using an aluminum rod (90 cm long) equipped with a rubber head (3.4 cm diameter). The top 5 cm of each core were removed by sliding a stainless steel blade across the top of the coring tube. Sediment slices were put in separate core tubes (with similar dimensions) stoppered at the bottom for incubation. Selection of the depth of core for experimentation was based on literature information that in most lakes, total phosphorus tends to be highest at the 0 to 5 cm surface layer and to decrease with depth (Hosomi et al. 1982; Bostrom and Petterson 1982). Some studies (e.g., Carignan and Lean 1991), however, have reported nutrient release to at least a depth of 50 to 100 cm.

Laboratory Incubation of Sediment Cores

Two sets of cores were incubated at room temperature. One set was aerated to simulate turbulence in the lake, while the other set was sealed with rubber cups and adhesive tapes at their tops to exclude gaseous exchange. The latter arrangement simulated conditions when mats of water hyacinth cover the lake surface and depress oxygen concentrations in the water column. Aeration of cores utilized aquaria air pumps to which plastic tubings were attached, and special care was taken to ensure that the

sediments were not resuspended. Water loss due to evaporation was compensated for with distilled-deionized water after every sampling. Dissolved oxygen (mg L^{-1}), temperature (^{o}C), pH and conductivity ($\mu S\ cm^{-1}$) were monitored using automated meters every seven days for 35 days starting at Day 1 (experiment initiation). At 7-day intervals, 50 mL of water was drawn from each tube using a 50 mL syringe fitted with plastic tubing (87 cm long x 0.9 cm internal diameter) and analyzed immediately for SRP ($\mu g\ L^{-1}$) following standard methods (APHA 1998) described in Chapter 2 of the current study. On Day 35, all the above parameters were recorded, the experiment was terminated, and the sediments were processed for TN and TP as described in Chapter 2. This experiment was repeated two times.

Phosphorus release rates were calculated from differences in P concentrations in the water column between successive sampling times (Stephen et al. 1997; Holdren and Armstrong 1980). Phosphorus release rates over time ($\Delta P/\Delta t$) were then calculated using Eq. 3-1 adopted from Stephen et al. (1997):

$$\text{Release rate (mg m}^{-2}\text{ day}^{-1}) = [C * H * 1000 * 24] \div i \qquad \text{(Eq.3-1)}$$

where C is change in concentration (mg L^{-1}) (concentration in overlying water at the end of incubation minus initial concentration); H is height of overlying water in meters; and i is incubation time in hours. The constant 1,000 is used to convert micrograms per liter to milligrams per liter; while 24 is to convert days into hours.

Since water hyacinth infested the bays differentially, its contribution to sediment characteristics, especially after its extensive sinking during late 1998, was assumed differential as well. One approach to evaluate this effect was to assess carbon content of sediments. Before infestation by water hyacinth, the main primary producers were

phytoplankton, but subsequent water-hyacinth dominance in sheltered littoral zones of Thruston Bay is thought to have replaced phytoplankton primary production. This likely led to a shift in carbon fixation and deposition as water hyacinth has more structural carbon than algae. Carbon content of sediments reflects differences in the dominant primary producer during and after water-hyacinth peak biomass cover.

Sediment samples were therefore collected from Thruston and Fielding bays close to the shore (60 m offshore) and at approximately 300 m offshore using the piston corer described above. Collection of samples was similar to that for nutrient-release experiments, and overlying water was decanted similarly. Each sediment core was sliced, using a stainless steel blade, into 1 cm slices down to 4 cm, and the sediment below 4 cm was discarded. Sediment slices were put on Plexiglas petri dishes and oven dried at 105 ^{o}C until constant weight was attained. Net dry weight was determined, and sediments were put in porcelain crucibles and ashed in a furnace at 550 ^{o}C for determination of loss on ignition (LOI). Carbon content was calculated by multiplying dry weight LOI by 45 % (Emerson et al. 1983).

Data on physicochemical parameters and P release were analyzed using General Linear Model (GLM) Repeated Measures Test of analysis, SPSS Version 10, while regular One-Way ANOVA was used for analyses of carbon content. Scheffe's Method of ANOVA (Scheffe', 1953) was used to identify significant differences ($P = 0.05$ and $P = 0.01$) through multiple comparison of means. Data that showed significant ($P < 0.05$ and $P < 0.01$) Mauchly's Test of Sphericity were transformed using natural logarithm (Ln) to homogenize variances.

Results

Physicochemical Parameters in the Water

Data for mean values of physicochemical parameters from overlying water for Experiments 1 and 2, are given in Figures 3-1 and 3-2, respectively, while statistical results are in Table 3-1 (before data transformation) and Table 3-2 (after data transformation). Total anoxia was not attained by eliminating air supply to nonaerated tubes since mean dissolved oxygen in aerated trials was almost double that in nonaerated trials (Figures 3-1 A and 3-2 A).

In Experiment 1, highly significant differences ($P < 0.01$) in dissolved oxygen concentrations (Figure 3-1 A) were due to within (time) effects. This was attributed to consistently low and consistently high dissolved oxygen in the nonaerated and aerated trials, respectively. There were also significant differences ($P < 0.05$) in concentration of dissolved oxygen due to interactive effects. Lack of significant treatment effects in Experiment 1 was probably due to failure to attain anoxia in nonaerated trials.

In Experiment 2, highly significant differences ($P < 0.01$) in dissolved oxygen (Figure 3-2 A) were attributed to time and treatment effects, while interactive effects resulted into significant effects ($P < 0.05$). Significantly lower concentrations were in nonaerated trials (range 4.0 to 4.4 mg L-1), while significantly higher values were in the aerated setup (range 6.4 to 8.0 mg L^{-1}).

In Experiment 1, temperature differences (Figures 3-1 B) were highly significant ($P < 0.01$) due to time and treatment effects, but interactive effects (between time and treatment) were marginally significant after data transformation. Significantly higher

mean temperatures were in the nonaerated (range 26.5 to 27.1 °C) than aerated trials (range 26.3 to 26.4 °C).

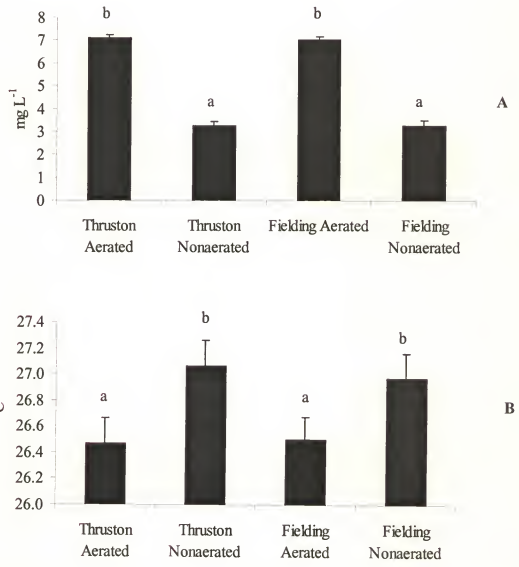


Figure 3-1. Physicochemical parameters for P release from sediments in Experiment 1. A) Dissolved oxygen (mg L^{-1}). B) Temperature (°C). C) pH. D) Conductivity (µS cm^{-1}).

In Experiment 2, temperature differences were highly significant ($P < 0.01$) over time, and significant ($P < 0.05$) over treatment, but interactive effects were not significant

($P > 0.01$, range 24.7 to 25.0 °C). Non significant interactive effects on temperature likely explain the lack of differences in overall mean temperatures (Figure 3-2 B).

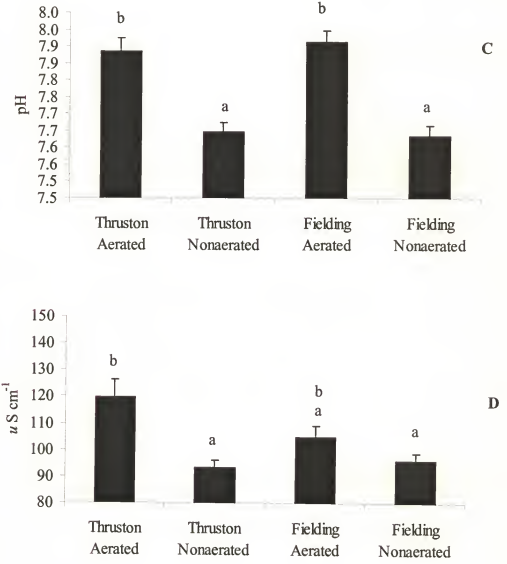


Figure 3-1. Continued

In Experiment 1, pH (Figure 3-1 C) differences were highly significant ($P < 0.01$) due to time and treatment effects, but interactive effects were not significant ($P > 0.05$). Aerated trials had significantly higher pH (range 7.9 to 8.0) than nonaerated trials (range

7.5 to 7.6). In Experiment 2 (Figure 3-2 C), there were no significant time, treatment, or interactive effects ($P > 0.01$, Tables 3-1 and 3-2) on pH (range 7.7 to 7.8)

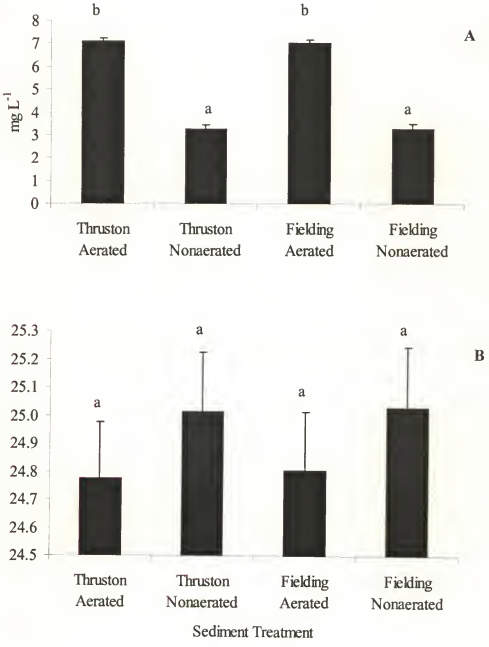


Figure 3-2. Physicochemical parameters for P release from sediments in Experiment 2. A) Dissolved oxygen (mg L^{-1}). B) Temperature (^{o}C). C) pH. D) Conductivity (($\mu S\ cm^{-1}$).

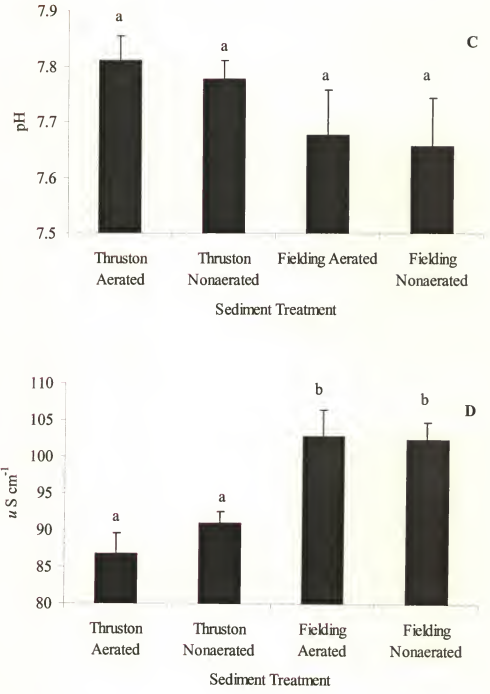


Figure 3-2. Continued

Figure 3-1 D shows average conductivity values for Experiment 1. There were highly significant ($P < 0.01$) time effects on conductivity (Tables 3-1 and 3-2).

Significantly higher mean conductivity was in aerated trials (range 105 to 120 $\mu S\ cm^{-1}$) than nonaerated trials (range 94 to 96 $\mu S\ cm^{-1}$). Conductivity in the aerated trial of Fielding Bay was, however, not significantly different from the significantly lower conductivity group. There were no significant treatment and interactive effects ($P > 0.01$) on conductivity in Experiment 1.

In Experiment 2, there were highly significant ($P < 0.01$, Tables 3-1 and 3-2) time effects on conductivity (Figure 3-2 D). Significantly lower values were from Thruston Bay (range 87 to 91 $\mu S\ cm^{-1}$), while Fielding had significantly higher conductivity (102 to 103 $\mu S\ cm^{-1}$). No significant ($P > 0.01$) treatment or interactive effects were noted (Tables 3-1 and 3-2) in Experiment 2.

Table 3-1. Probabilities resulting from Repeated Measures Test on differences in treatment (aerated vs nonaerated) for water column physicochemical parameters during P release from sediments using untransformed data

	Within-effects (Time)	Between-effects (Treatment)	Interactive-effects	Variance Test
Experiment 1				
D.O.	0.000	0.123	0.043	0.197
Temp.	0.000	0.000	0.048	0.000*
pH	0.000	0.006	0.888	0.766
Cond.	0.000	0.768	0.277	0.000*
SRP	0.178	0.016	0.910	0.000*
Release Rate	0.946	0.152	0.528	0.145
Experiment 2				
D.O.	0.000	0.000	0.003	0.020*
Temp.	0.000	0.024	0.226	0.023*
pH	0.102	0.351	0.570	0.000*
Cond.	0.000	0.608	0.638	0.000*
SRP	0.000	0.688	0.998	0.000*
Release Rate	0.951	0.812	0.882	0.041*

NB: * Unequal Variances hence require Ln transformation.

Table 3-2. Probabilities resulting from Repeated Measures Test on differences in treatment (aerated vs nonaerated) for water column physicochemical parameters during P release from sediments using Ln transformed data

	Within-effects (Time)	Between-effects (Treatment)	Interactive-effects	Variance Test
Experiment 1				
D.O.	0.000	0.224	0.020	0.069
Temp.	0.000	0.000	0.062	0.369
pH	0.000	0.006	0.893	0.780
Cond.	0.000	0.661	0.118	0.071
SRP	0.587	0.000	0.607	0.323
Experiment 2				
D.O.	0.000	0.006	0.027	0.054
Temp.	0.000	0.024	0.285	0.108
pH	0.107	0.352	0.556	0.211
Cond.	0.000	0.545	0.599	0.073
SRP	0.000	0.475	0.990	0.091

Phosphorus Release from Sediments

Mean values for water column SRP concentrations in incubation tubes for Experiments 1 and 2 during P release from sediments are given in Figure 3-3. In Experiment 1, there were no significant differences ($P > 0.05$) in the mean concentrations of SRP (Figure 3-3 A) among all trials due to time, and interactive effects between time and treatment (Tables 3-1 and 3-2). However, treatment effects were significant ($P < 0.05$) before (Table 3-1), and highly significant ($P < 0.01$) after data transformation (Table 3-2), with a significantly higher ($P < 0.05$) overall mean from aerated sediments of Thruston Bay (110.5 ± 30.8 $\mu g\ L^{-1}$).

In Experiment 2, highly significant differences ($P < 0.01$) in mean SRP concentrations were due to time effects, while treatment and interactive effects were not significant ($P > 0.01$, Tables 3-1 and 3-2). Mean concentrations of SRP in the water column (Figure 3-1 B) were significantly higher in aerated sediments from Thruston Bay

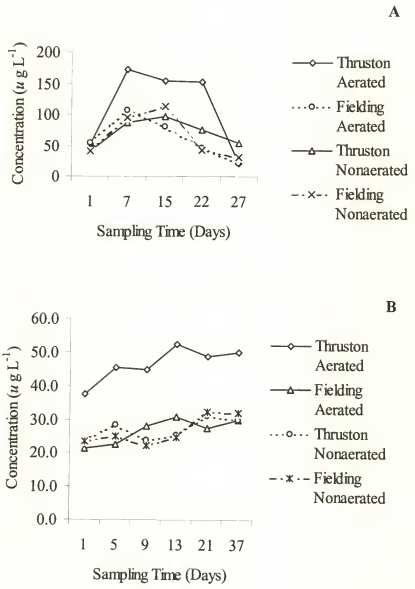


Figure 3-3. SRP concentration in the water column of incubation tubes. A) Experiment 1. B) Experiment 2.

(range 37.5 to 52.3 μg L^{-1}) than in the rest of the trials (range 21.5 to 32.3 μg L^{-1}). Higher concentrations of SRP in the aerated trials than the nonaerated setups for Thruston Bay contradict the widely held view of significantly higher P release under hypoxic or anoxic conditions (Togwell and Schindler 1975; Lovely 1991; Friese et al. 1998).

Pearson's correlation coefficients (r) between physicochemical parameters and SRP concentrations in the water column are given in Table 3-3. In most trials, no apparent correlation was noted, although others assert that significantly higher P is released under anaerobic conditions (Togwell and Schindler 1975; Friese et al. 1998); in this study, total anoxia was not attained (e.g., lowest mean dissolved oxygen concentrations recorded in nonaerated trials were 1.8 mg L^{-1} in Experiment 1 and 0.7 mg L^{-1} in Experiment 2). It is possible that such trace amounts of dissolved oxygen could render the experimental setup

Table 3-3. Pearson's Correlation Coefficients (r) between SRP in Experiments 1 and 2 and physicochemical parameters

		Experiment 1 (n = 20)		Experiment 2 (n = 20)	
Parameter	Bay	r	Significance	r	Significance
(A) Aerated trials					
Dissolved oxygen and SRP	Thruston	-0.28	0.32	0.08	0.75
	Fielding	-0.22	0.43	0.36	0.12
Temperature and SRP	Thruston	0.24	0.38	0.11	0.65
	Fielding	0.55*	0.03	0.49*	0.03
pH and SRP Aerated	Thruston	0.33	0.24	0.19	0.42
	Fielding	0.70**	0.00	0.19	0.43
Conductivity and SRP	Thruston	-0.12	0.67	-0.77**	0.00
	Fielding	-0.11	0.69	-0.14	0.56
(B) Nonaerated trials					
Dissolved oxygen and SRP	Thruston	-0.33	0.23	-0.42	0.07
	Fielding	-0.32	0.25	-0.27	0.26
Temperature and SRP	Thruston	0.20	0.48	0.20	0.40
	Fielding	0.62*	0.01	0.14	0.56
pH and SRP Aerated	Thruston	0.48	0.07	-0.10	0.69
	Fielding	0.34	0.21	-0.33	0.15
Conductivity and SRP	Thruston	0.01	0.98	-0.49*	0.03
	Fielding	0.33	0.24	0.06	0.81

* Significant at P = 0.05 (2-Tailed); ** Significant at P = 0.01 (2-Tailed).

to behave like the aerated trials, resulting in binding of P to oxidized cations (Fe, Al, and Mn). In aerated trials, however, significant correlations were noted between temperature and SRP concentrations for Fielding Bay sediments in both Experiments 1 (r = 0.55, P =

0.05) and 2 (r = 0.49, P = 0.05), between pH and SRP in Experiment 1 for Fielding Bay sediments (r = 0.70, P = 0.01), and between conductivity and SRP in Experiment 1 (r = -0.77, P = 0.01). Among the nonaerated trials, significant correlations were noted between temperature and SRP in Experiment 1 for Fielding Bay sediments (r = 0.62, P = 0.05) and between conductivity and SRP in Experiment 2 for Thruston Bay sediments (r = -0.49, p = 0.05).

Release rates of SRP from sediments in Experiments 1 and 2 are given in Figure 3-4. The following observations were made

- **Experiment 1**. Phosphorus release rates (Figure 3-4 A) increased in all setups until Day 10 when maximum rates were attained, and thereafter, rates declined profoundly. No significant differences (P > 0.01, Tables 3-1) in P release rates (range –9.7 to 8.8 mg m^{-2} day^{-1}) due to time and treatment effects, and interactions between these two effects were, however, noted among all trials.

- **Experiment 2.** Phosphorus release rates (Figure 3-3 B) fluctuated for most of the experimental period but started declining profoundly after Day 15. Fluctuations became less profound between Day 21 and Day 37. There were, however, no significant differences (P > 0.01, Table 3-1) in release rates (range -1.8 to 3.9 mg m^{-2} day^{-1}) among all trials.

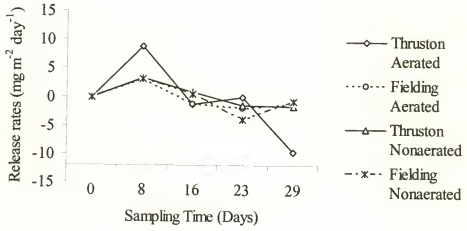


Figure 3-4. Phosphorus release rates from sediments. A) Experiment 1. B) Experiment 2.

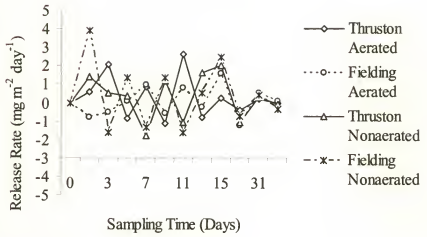


Figure 3-4. Continued.

Carbon Content in Sediments

Mean carbon content along depth profiles in sediments from Thruston and Fielding bays are given in Figure 3-5. At all sites, there were no significant differences ($P > 0.05$) in carbon content of sediments along depth profiles. For

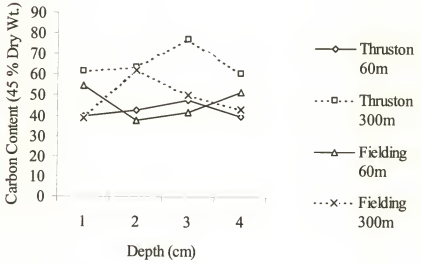


Figure 3-5. Depth profiles of sediment carbon content (≅ 45 % Dry Wt.).

example, in Thruston Bay sediments, carbon content was in the range 39.6 to 47.7 and 60.8 to 77.2 % dry wt at 60 and 300 m offshore, respectively. In Fielding Bay, values were in the range 37.8 to 54.9 and 38.6 to 62.4 % dry wt at 60 and 300 m offshore, respectively. Overall mean carbon content from each site showed significantly higher ($P < 0.05$) carbon in sediments at 300 m offshore in Thruston Bay (65.8 ± 12.7 % dry wt.), while values were significantly lower at other sites (range 42.4 to 48.6 % dry wt.).

Discussion

Factors Influencing Phosphorus Release from Sediments

Phosphorus flux between surface sediments and the water column is a continuous process and is influenced by various factors including concentration gradients, redox potential, mixing patterns, resuspension, bioturbation, bacterial activity, temperature and sediment composition (Premazzi and Provini 1985). Phosphorus release from sediments is common in shallow lakes (Mayer et al. 1999) and littoral zones of deep lakes. Phosphorus released into the porewater through solubilization and decomposition processes can be released into the water column through such transport mechanisms as diffusion and advection resulting from turbulence due to bioturbation, gas ebullition and wind/wave action, promoting sediment resuspension.

Enhanced release of P from sediments under anaerobic conditions is well documented (Togwell and Schindler 1975; Lovely 1991; Friese et al. 1998). Presence of an anaerobic layer at the sediment-water interface and an anoxic water column lead to reduction of Fe^{3+} to Fe^{2+} and liberation of chemically bound P. It is likely that Fe is available in clay sediments as evidenced by a brown coloration when sediments were

exposed to air; the brown coloration was likely oxidized Fe (Fe^{3+}). There was however, no data on sediment Fe from sampling sites in Lake Victoria. During this study, sediment cores that were not aerated did not attain total anoxia in the water column and probably also at the sediment-water interface. Physicochemical data were not taken at the sediment-water interface to avoid disturbance of the sediment surface layer via sediment resuspension. Absence of total anoxic conditions in nonaerated trials minimized differences in release rates between aerated and nonaerated cores and likely accounted for limited P release commonly reported for aerobic conditions.

In related studies, James et al. (1996) and Chengxin et al. (1996) found that P release from sediments was double under anoxic conditions as a result of adjusting pH of the overlying water from 8.5 to 9.0. Their laboratory rates increased to a maximum of 23 mg $m^{-2}day^{-1}$ under anoxic conditions. Further, Serruya et al. (1974) found P release rates as high as 0.8 mg m^{-2} day^{-1}, while Hu et al. (2001) found maximum release rates as high as 15 mg m^{-2} day^{-1} under anaerobic conditions. In this study, the highest release rates from sediments under depressed oxygen conditions were 3.3 ± 0.6 mg m^{-2} day^{-1} for Thruston Bay and 3.8 ± 0.4 mg m^{-2} day^{-1} for Fielding Bay in nonaerated sediments.

Soerjani (1987) demonstrated that even under hypertrophic conditions, sediments could contribute an average of 72 % of all phosphorus taken up by growth of submerged macrophytes, thus identifying sediments as potential nutrient sources for the open water. In the current study, P release even under well oxygenated, in addition to hypoxic conditions, is a manifestation that P release occurs at various environmental conditions (especially of dissolved oxygen). It is therefore likely that proliferation of water hyacinth in most bays, including zones with minimal shelter for plant establishment (e.g.,

Macdonald and Hannington), could have been a result of continuous P release to the water column despite high levels of dissolved oxygen (through phytoplankton recharge and diffusion from the atmosphere). In the Nakivubo Channel of Murchison Bay and at the Katonga River inflow, where anoxic conditions prevail for most the year, to favor denitrification, NO_3-N and Fe^{3+} concentrations are expected to be relatively low, leading to immobilization of P. Nonaeration, simulating depressed oxygen as in polluted waters, under extensive water hyacinth mats, and in the hypolimnia of eutrophic waters, was expected to enhance P release from sediments. If this occurs in sheltered waters infested with water hyacinth, further proliferation due to favorable P regimes is likely if water hyacinth control measures are not taken. Coupled with nutrient loading to the littoral zones of the lake, especially through sewage inflow and soil erosion from the catchment, problems with aquatic plants in general and water hyacinth in particular are bound to remain.

Kleenberg et al. (2001) found that NO_3-N (> 1,000 $\mu g\ L^{-1}$) can buffer the redox potential of surface sediments under low oxygen conditions. They found that this N concentration is high enough to prevent release of iron-bound phosphate. Serruya et al. (1974) found that exchangeable P was mainly a Fe-bound fraction that was released when Fe precipitated with sulfide under very low redox potential. Low dissolved oxygen in nonaerated trials, coupled with a brown iron rust precipitate (assumed to be compounds of Fe^{3+}) at the interface between the sediments and the incubation tubes, was likely an indication of oxidized Fe that was capable of releasing P under hypoxic to anoxic conditions. However, it was not possible to undertake a confirmatory test for the quality of the brown precipitate.

Another environmental factor that may influence P flux between surface sediments and the water column is pH. Bostrom and Petterson (1982) found high P release in the pH range 8 to 10, with maxima at pH 9. They also found that increased pH decreased the ability of NO_3-N to retain P in the sediments. The mean pH values recorded during this study were circumneutral, with the highest being 7.9 ± 0.0 for Experiment 1 and 7.8 ± 0.0 for Experiment 2. These values could have accounted for the low release rates probably by increasing the ability of oxidized N to keep P in the sediments.

A portion of the increase in SRP concentrations in the overlying water may result from mineralization of dissolved organic P (DOP), rather than P release from sediments. This could not be verified since DOP was not quantified. However, if increases in SRP are accompanied by similar increases in TP, it is probable that mineralization of DOP contributes an insignificant fraction. In surface sediments that have high microbial activity, a high oxygen demand leading to anoxic conditions at the sediment-water interface may be created. Under such conditions, there can be enhanced P release from sediments, although a sizeable fraction is likely to be converted to organic P through assimilation by microbes.

Under natural conditions, increased temperature may lead to increased P release. This may have an indirect influence through increased microbial activity in the sediments. Temperature values recorded during this study (range 24 to 27 °C) were within ranges found in tropical lakes such as Lake Victoria. Positive significant correlations ($P = 0.05$, Table 3-5) between SRP concentrations in both aerated and nonaerated trials of sediments from Fielding Bay (Experiment 1), aerated trials of Fielding Bay (Experiment 2), are likely indications of the significance of temperature in P

release from sediments. This is further supported by the significantly different temperatures between aerated and nonaerated trials of both experiments due to time and treatment effects (Tables 3-1 and 3-2).

Under natural situations, bioturbation due to benthic organisms may result in enhanced P release. Burrowing of benthic organisms increases the depth at which dissolved oxygen is distributed in surface sediments. This leads to an increase in available anoxic (or hypoxic) and oxic microsites within the sediments. Alteration of redox potential due to presence of these microsites influences release of chemically bound P (Lovely 1991). In shallow aquatic systems with diurnal mixing, the rate of P cycling is expected to be high since sediments are continuously brought into circulation (Reddy and Gale 1994). Aeration of the water column is thought to have increased the amount of dissolved oxygen in contact with the sediment surface, and subsequent diffusion into the surface sediment layers along a concentration gradient. This was considered to some extent similar to bioturbation, and was thought to increase alternate oxic-anoxic microsites in surface sediment. However, care was taken not to resuspend sediments, an approach that limited the magnitude of oxygen delivery further down the sediments, and is thought to have contributed to the minimal amounts of P released into the water column.

Carbon Content in Sediments

Although no significant differences were found in sediment carbon content between the two bays at respective depths, the slightly high values for Thruston Bay sediments are likely due to the huge hyacinth biomass that occurred in this bay for a longer time and later sank to the lake bottom. This was supported by the significantly higher overall mean

(all depth data combined for each site in each bay) in Thruston than in Fielding Bay. The general trend was an increase in carbon content with depth (at least down to 3 cm), and is likely due to accumulation of recalcitrant materials resistant to decomposition such as lignin and wax (Battle and Mihuc 2000). Unfortunately, data for this study were collected four years after the water hyacinth biomass sank; it would have been convenient if there were consistent data collected before, during, and after water hyacinth demise for addressing the issue.

Conclusions

Results on P release from sediments during the current study seem conflicting. For example, lack of significant differences (due to time effects) in Experiment 1 and highly significant differences in Experiment 2, on mean SRP concentration in the water column makes it difficult to draw conclusions. Similar contradictory observations were noted with respect to treatment effects, where there were highly significant differences in Experiment 1 and no significant differences in Experiment 2. However, lack of significant differences due to time and treatment effects, and due to interactions between these two effects indicated that P released from sediments could not be attributed to the differential patterns of water hyacinth infestation that occurred in the two bays. On the contrary, considering the arithmetic means of SRP concentrations from sediments of both sources, sediments of Thruston Bay released greater amounts of P compared to those of Fielding Bay. Whether these differences are due to human activities that led to P loading such as use of fertilizers within the catchment, or were due to sunken water hyacinth is difficult to ascertain since this study was undertaken four years after the massive collapse of water hyacinth that occurred in late 1998. It is possible that effects of sunken water

hyacinth have been modified over time, since decomposition of organic matter of aquatic macrophyte origin such as water hyacinth, as will be demonstrated in Chapter 4, takes a relatively shorter time to decompose fully. It is unlikely that recalcitrant materials of plant origin (e.g., cutin, chitin, wax, and lignin) can account for a significant proportion of P released into the water column from sediments.

When considering control options for aquatic macrophytes such as water hyacinth, nutrient release from sediments is of critical importance in sheltered shallow bays, since it is here that nutrient fluxes between sediments and the water column are maximal due, in part, to shallow depth, sediment resuspension by winds/waves, and bioturbation. It is also in littoral zones that effects of allochthonous nutrient loading are manifest.

Phosphorus release from sediments of Lake Victoria should be assessed under different environmental conditions such as NO_3-N, pH and conductivity in order to predict likely effects of P fluxes on water quality.

Other aquatic plants such as Najas horrida occur in some littoral areas of Lake Victoria and the Kyoga-minor lakes. There is need to assess the role of nutrient release from sediments and how this influences proliferation of these potentially invasive macrophytes.

CHAPTER 4
PHOSPHORUS RELEASE FROM DECOMPOSING WATER HYACINTHS

Introduction

Decomposition of aquatic macrophytes can influence carbon cycling and energy flow in shallow, aquatic ecosystems considerably (Battle and Mihuc 2000). The breakdown of organic matter releases inorganic components including nutrients that were chemically incorporated in plant tissues. This mineralization process is enhanced by high organic phosphorus content and occupation of most sorption sites on organic and inorganic particles of surface sediments results in a low sorption capacity (Bostrom and Petterson 1982). Of the P transfer mechanisms, organic matter deposition at the sediment surface is considered very important (Bostrom 1988). A few investigations have demonstrated the importance of internal processes for nutrient cycling in tropical lakes including decomposition of aquatic macrophytes (Pieczynska 1990). Water hyacinth usually has high production rates that may reach 40 t ha^{-1} y^{-1} (DeBusk et al. 1981). However, few studies have examined biomass turnover of this plant (Gopal 1987) relative to nutrient cycling in tropical aquatic ecosystems.

Decomposition studies of other aquatic macrophytes such as Salvinia sp. indicated that nutrient release was rapid during the initial 4 days and was attributed to physical leaching (Ogwada et al. 1984; Sharma and Goel 1986). This was followed by slow nutrient release attributed to microbial decomposition. Sain (1984), however, reported rapid release of nutrients from decomposing wild rice (Zizania aquatica) during the first 3 weeks

followed by slow release thereafter. Reddy and DeBusk (1991) studied decomposition of water hyacinth detritus in situ and found higher decomposition rates in the root zone than at the sediment-water interface. Under laboratory conditions, Reddy and Sacco (1981) found higher rates of SRP release under anaerobic than aerobic conditions. They also found that after herbicide application that resulted in death of water hyacinth in a canal, there were higher concentrations of soluble N and P in the canal drainage water than before herbicide application.

The objective of this study was to assess, under laboratory conditions, P release rates from decomposing water hyacinths under aerobic and hypoxic conditions and to monitor influences of decomposition products on water quality.

Materials and Methods

Laboratory Incubation

Water hyacinth plants with minimal weevil infestation (i.e., < 10 feeding marks) were collected from Lake Victoria and used for assessing P release rates during decomposition. Plants were washed in tap water to remove attached debris, cut into pieces approximately 1 cm^2 using a stainless steel blade and mixed thoroughly by hand. Subsamples of 50 g were weighed on an electronic balance (precision of 0.01 g) and put in triplicate sets of Plexiglas tubes (83 cm x 6.7 cm) containing 1.6 L of lake water. Howard and Howard (1978) used a plant:water ratio of 1 g plant material:30 mL water for Typha domingensis when investigating nutrient release via decomposition. The plant:water ratio used during this study (1 g plant:32 ml water) was considered comparable to that of other investigations.

Control tests employed the same setup but without water hyacinth. Both experimental and control setups were incubated at room temperature. One set was aerated to simulate turbulence in the absence of extensive water hyacinth mats on the lake, while in the other,

incubation tubes were sealed with rubber stoppers and adhesive tape to eliminate gaseous exchange. The latter arrangement simulated conditions when extensive mats of water hyacinth cover the lake surface and depressed dissolved oxygen conditions develop in the water column.

Aeration was done using aquaria air pumps to which plastic tubes were attached and supplied air to the incubation tubes. Water loss due to evaporation was compensated for with distilled-deionized water after every sample event. Dissolved oxygen (mg L^{-1}), temperature (^{o}C), pH, and conductivity ($\mu S\ cm^{-1}$) were monitored using automated meters at least every 2 days just before taking water samples for nutrient analyses. At 2-day intervals, 50 mL of water were withdrawn from each tube using a 50 mL syringe fitted with plastic tubing (87 cm long and 0.9 cm internal diameter) and analyzed immediately for SRP ($\mu g\ L^{-1}$) following methods described in APHA (1989). The experiment was repeated two times, and each trial lasted 28 to 38 days. Howard and Howard (1978) did a similar experiment that lasted 144 days using Typha domingensis and found significant weight loss during the initial 3 days of the experiment similarly to William (1970) on leaves of Acer rubrum L., Liriodendron tulipifera L. and Quercus alba L.

Monitoring changes in pH, conductivity and various ions gives an indication of changes in water chemistry (Howard and Howard 1978) during decomposition. During this study, changes in water chemistry were monitored by measuring changes in dissolved oxygen, temperature, pH and conductivity using automated portable meters.

Soluble phosphorus (SRP) release rates were calculated from differences between SRP concentrations in the water column between successive sampling dates (Stephen et

al.1997; Holdren and Armstrong 1980). Phosphorus release rates over time ($\Delta P/\Delta t$) were then calculated using Eq. 4-1 adopted from Stephen et al. (1997).

$$\text{Release Rates } (\text{mgm}^{-2}\text{day}^{-1}) = [C * H * 1000 * 24] \div i \qquad \text{(Eq. 4-1)}$$

where C is change in P concentration (mg L^{-1}) (i.e., concentration in overlying water at the end of incubation minus initial concentration); H is height of overlying water in meters; and i is incubation time in hours. Repeated Measures One-Way ANOVA was used to identify significant differences in physicochemical parameters (dissolved oxygen, temperature, pH and conductivity), and P release (Scheffe', 1953) through multiple comparison of means. Data whose Mauchly's Test of Sphericity were significant ($P < 0.05$), were transformed using natural logarithm to homogenize variances.

Results

Physicochemical Parameters

Data on physicochemical parameters in the water column of incubation tubes are given in Figures 4-1 and 4-2 for Experiments 1 and 2, respectively. In Experiment 1, treatment effects, in addition to interactive effects between treatment and time did not have significant differences ($P > 0.01$) on dissolved oxygen among trials. However, highly significant differences ($P < 0.01$) were due to time effects (Tables 4-1 and 4-2), with significantly lower dissolved oxygen occurring in the nonaerated trials with hyacinth (Figure 4-1 A). By Day 7, dissolved oxygen in the nonaerated trials with hyacinth had dropped to 0.7 mg L^{-1} from 6.3 mg L^{-1} recorded on Day 1. Concentration in the nonaerated trials without hyacinth did not significantly differ from that in aerated ones with or without hyacinth (range 4.4 to 7.6 mg L^{-1}).

In Experiment 2, highly significant differences ($P < 0.01$) in dissolved oxygen (Figure 4-2 A) were due to time and treatment effects. Interactive effects between time

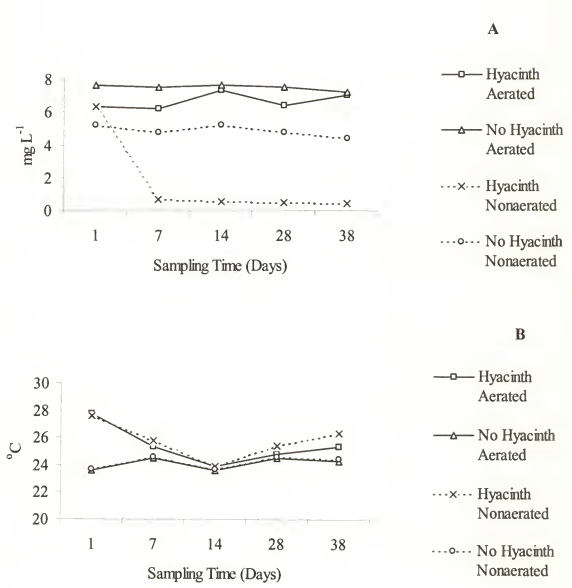


Figure 4-1. Physicochemical parameters in the water column, Experiment 2. A) Dissolved oxygen (mg L^{-1}). B) Temperature (^{o}C). C) pH. D) Conductivity ($\mu S\ cm^{-1}$).

and treatment were, however, not significant ($P > 0.05$) after data transformation (Tables 4-1 and 4-2). Like in Experiment 1, significantly lower oxygen was in the nonaerated trials with hyacinth (range 0.3 to 0.9 mg L^{-1}), while the rest of the trials did not significantly differ (range 3.6 to 7.9 mg L^{-1}) from each other.

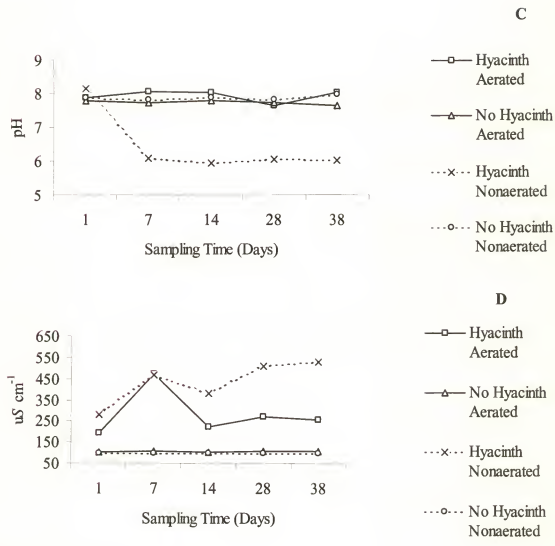


Figure 4-1. Continued

In Experiment 1, there were no significant treatment and interactive effects ($P > 0.05$) on temperature (Tables 4-1 and 4-2), although highly significant effects ($P < 0.01$) were noted over time. Trials without hyacinth had lower temperatures compared to those with hyacinth (Figure 4-1 B). In Experiment 2, highly significant differences ($P < 0.01$) in temperature were due to time effects, while treatment effects were just significant ($P < 0.05$). No significant interactive effects on temperature were noted in Experiment 2 (Tables 4-1 and 4-2). Aeration resulted in lowering temperature over time, although

nonaerated trials fluctuated similarly (Figure 4-2 B). In addition, more pronounced temperature fluctuations occurred in Experiment 2 (Figure 4-2 B) compared to Experiment 1 (Figure 4-1 B).

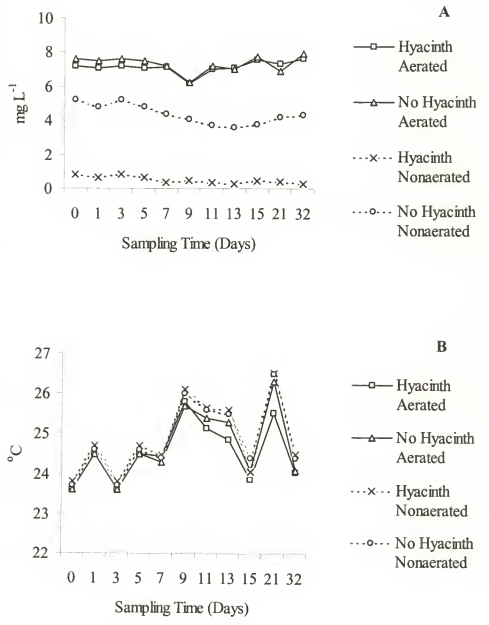


Figure 4-2. Physicochemical parameters in the water column, Experiment 3. A) Dissolved oxygen (mg L^{-1}). B) Temperature (°C). C) pH. D) Conductivity (µS cm^{-1}).

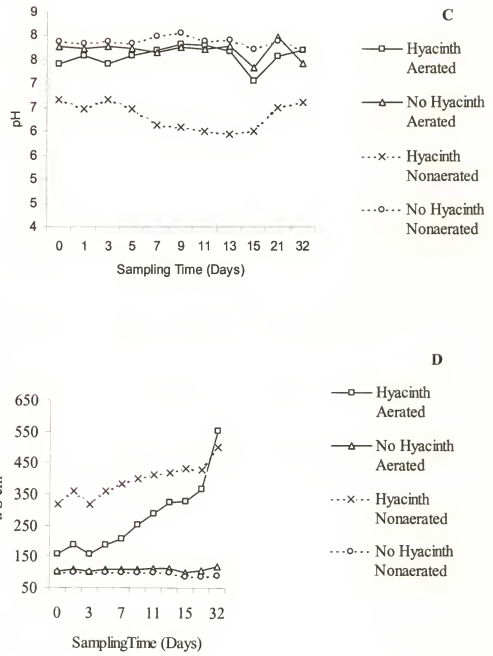


Figure 4-2. Continued

In Experiment 1, highly significant time effects ($P < 0.01$, Tables 4-1 and 4-2) resulted in low pH in nonaerated trials with hyacinth than in other trials (Figure 4-1 C). Similar observations were made on pH in Experiment 2, although interactive effects were

Table 4-1. Probabilities resulting from Repeated Measures Test on differences in treatment (aerated vs nonaerated) for water column physicochemical parameters during P release from decaying water hyacinth using untransformed data

	Within effects	Between effects	Interactive effects	Variance Test
Experiment 1				
D.O.	0.000	0.692	0.942	0.035*
Temp.	0.000	0.914	0.997	0.000*
pH	0.000	0.984	0.999	0.000*
Cond.	0.000	0.852	0.977	0.000*
SRP	0.000	0.000	0.000	0.000*
Release Rate	0.498	0.430	0.732	0.000*
Experiment 2				
D.O.	0.000	0.003	0.032	0.013*
Temp.	0.000	0.019	0.860	0.000*
pH	0.000	0.486	0.080	0.009*
Cond.	0.000	0.256	0.838	0.000*
SRP	0.000	0.002	0.000	0.000*
Release Rate	0.003	0.165	0.013	0.000*

* Nonhomogeneous variances hence requires Ln data transformation

Table 4-2. Probabilities resulting from Repeated Measures Test on differences in treatment (aerated vs nonaerated) for water column physicochemical parameters during P release from decaying water hyacinth using transformed data

	Within effects	Between effects	Interactive effects	Variance Test
Experiment 1				
D.O.	0.000	0.066	0.180	0.063
Temp.	0.000	0.886	0.997	0.055
pH	0.000	0.994	0.986	0.102
Cond.	0.000	0.716	0.826	0.079
SRP	0.000	0.003	0.000	0.088
Experiment 2				
D.O.	0.000	0.009	0.217	0.061
Temp.	0.001	0.019	0.902	0.070
pH	0.000	0.480	0.025	0.078
Cond.	0.000	0.128	0.809	0.109
SRP	0.000	0.000	0.000	0.091

as well significant ($P < 0.05$). Thus, pH was significantly lower in nonaerated trials with hyacinth, compared to others with or without hyacinth (Figure 4-2 C).

Conductivity in Experiment 1 had highly significant ($P < 0.01$) time effects (Tables 4-1 and 4-2), but treatment and interactive effects were not significant ($P > 0.05$). Over time, significantly higher conductivity was in nonaerated trials with hyacinth, while it was significantly lower in all trials without hyacinth (Figure 4-1 D).

Conductivity data for Experiment 2 are given in Figure 4-2 D. Similar trends were noted as in Experiment 1, with highly significant ($P < 0.01$) time effects, particularly in trials with hyacinth. Conductivity values in nonaerated trials were higher than in aerated trials, but were significantly lower in trials without hyacinth.

Concentrations of SRP in the Water Column

Concentrations of SRP in the water column for Experiment 1 are given in Figure 4-3. Although data indicate SRP values for 15 days, the experiment lasted up to 38 days. Data for the period after Day 15 are not included because concentrations of SRP had attained plateaus resulting in fairly constant values; thus it was deemed unnecessary to include such data. In the nonaerated trials of Experiment 1, mean concentrations of SRP increased profoundly between Days 3 and 4. By Day 5, concentrations had started leveling off, with average maximum concentrations in the plateau region (2871.4 ± 71.2 $\mu g\ L^{-1}$) attained on Day 10 (Figure 4-3). In aerated trials with hyacinth in Experiment 1, mean peak concentration (2041.1 ± 105.5 $\mu g\ L^{-1}$) was attained on Day 9, before dropping to its lowest (516.1 ± 51.0 $\mu g\ L^{-1}$) on Day 12. Differences in concentrations of SRP in the water column were highly significant ($P < 0.01$) due to time, treatment, and interactive effects (Tables 4-1 and 4-2). Thus, over time, significantly higher concentrations were recorded in trials with, than without hyacinth. Also, significantly higher concentrations were recorded in nonaerated trials with than aerated trials without hyacinth (Figure 4-3).

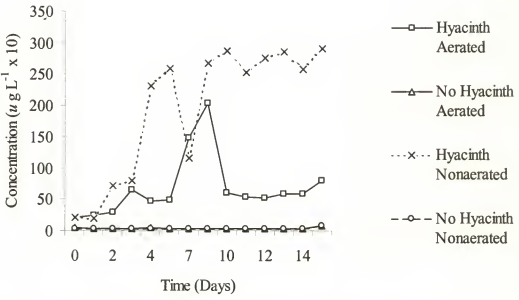


Figure 4-3. Mean concentrations of SRP in the water column, Experiment 1

Mean concentrations of SRP in the water column for Experiment 2 are given in Figure 4-4. In trials with hyacinth, mean concentrations peaked in the nonaerated trials on Day 5 (1224.1 ± 95.5 μg L^{-1}), and in aerated setups on Day 15 (487.9 ± 33.9 μg L^{-1}). In the former, there was a profound decline in concentrations after Day 5 to 842.5 ± 143.1 μg L^{-1} on Day 7, before fluctuating between 600 μg L^{-1} and 900 μg L^{-1} by termination of the experiment. In the aerated trials with hyacinth, average increase in SRP concentrations was gradual, but with the steepest slope between Days 9 and 11. Highly significant differences ($P < 0.01$) were due time and treatment effects, in addition to interactive effects between time and treatment (Tables 4-1 and 4-2).

Using regular One-Way ANOVA, it was noted that SRP concentrations in trials without hyacinth were significantly lower ($P < 0.01$) (range 19.5 to 36.6 μg L^{-1}), with no

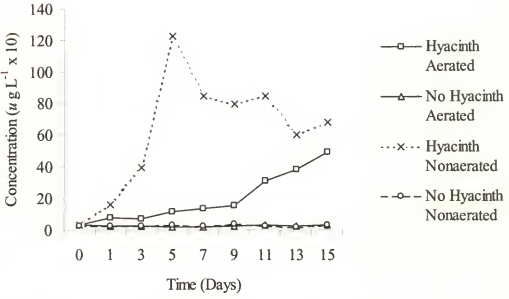


Figure 4-4. Mean concentrations of SRP in the water column, Experiment 2

significant differences between them. In trials with hyacinth, mean SRP concentration in aerated setups (341.4 ± 42.9 μg L^{-1}) was significantly lower ($P < 0.01$) than the nonaerated (650.0 ± 52.5 μg L^{-1}).

In both Experiments 1 and 2, there were highly significant effects ($P < 0.01$) of time, treatments, and interaction between the two, with hypoxic conditions enhancing P release more than well oxygenated conditions, and treatments with hyacinth released more P than those without hyacinth.

Correlation between Physicochemical Parameters and SRP Concentration

Pearson's correlation coefficients between mean SRP concentrations and physicochemical parameters in the water column for Experiments 1 and 2 are given in Table 4-3. No strong correlations were noted between physicochemical parameters and

trials, correlation was significant ($P < 0.05$) only between dissolved oxygen and SRP ($r = -0.53$, $P = 0.05$).

Table 4-3. Pearson's Correlation Coefficients (r) between water column physicochemical parameters and SRP concentration

	Experiment 2		Experiment 3	
Parameter	r	Significance	r	Significance
(A) Aerated Trials				
Dissolved Oxygen & SRP	0.18	0.44	0.45**	0.00
Temperature & SRP	-0.35	0.13	0.30*	0.05
pH & SRP	0.05	0.83	0.04	0.80
Conductivity & SRP	0.03	0.89	0.87**	0.00
(B) Nonaerated Trials				
Dissolved Oxygen & SRP	-0.53*	0.02	0.14	0.37
Temperature & SRP	-0.01	0.97	-0.22	0.15
pH & SRP	-0.03	0.90	0.13	0.40
Conductivity & SRP	-0.13	0.60	0.06	0.71

* Significant at P = 0.05 (2-Tailed); ** Significant at P = 0.01 (2-Tailed)

In aerated trials of Experiment 2, correlations were significant between SRP concentration and dissolved ($r = +0.45$, $P = 0.01$), between SRP and temperature ($r = +0.30$, $P = 0.05$), and between SRP and conductivity ($r = +0.87$, $P = 0.01$). Correlation between pH and SRP concentration ($r = 0.04$) was, however, not significant. In nonaerated trials, no significant correlations were noted.

Phosphorus Release Rates

Release rates of P from decomposing hyacinths for Experiment 1 are given in Figures 4-5. The maximum rate in the nonaerated trial (662.8 ± 91.9 mg m^{-2} day^{-1}) was attained on Day 4, compared to 217.7 ± 92.9 mg m^{-2} day^{-1} on Day 7 for the aerated trial. After Day 4 in the nonaerated trial, release rates declined profoundly, with the lowest being -317.2 ± 118.2 mg m^{-2} day^{-1} on Day 7 and thereafter, rates fluctuated in the range -15.6 and 144.6 mg m^{-2} day^{-1}. In aerated trials, the lowest mean rate was -635.6 ± 413.7

mg m^{-2} day^{-1} on Day 9, and thereafter, fluctuations became less profound (range –28.3 to 29.8 mg m^{-2} day^{-1}). In trials without hyacinth, release rates were lower than trials with hyacinth (range -24.2 to 3.7 mg m^{-2} day^{-1}). No significant differences ($P > 0.01$) were however, noted in P release rates among trials (Table 4-1).

Phosphorus release rates from decomposing hyacinths for Experiment 2 are given in Figure 4-6. Maximum mean release rate in the nonaerated trials with hyacinth was 182.6 ± 36.9 mg m^{-2} day^{-1} and occurred on Day 6, before reaching its lowest (-83.9 ± 52.1 mg m^{-2} day^{-1}) on Day 8. In nonaerated trials without hyacinth the range was -0.6 to 2.2 mg m^{-2} day^{-1}, with minimal variations compared to that with hyacinth.

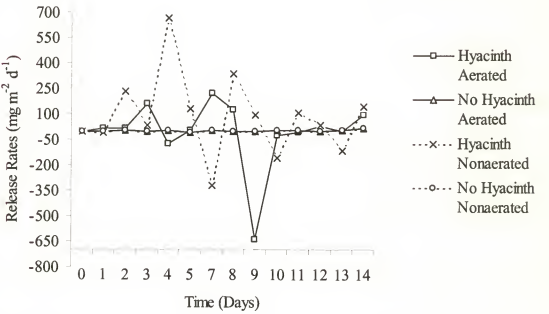


Figure 4-5. Phosphorus release rates from decomposing hyacinths, Experiment 2

In the aerated trials with hyacinth, highest mean release rate (18.5 ± 2.4 mg m^{-2} day^{-1}) occurred on Day 2, and by Day 4, the rate had reached its lowest value (-0.3 ± 2.0

mg m^{-2} day^{-1}). In aerated trials without hyacinth, the rates were in the range –4.6 to 0.8 mg m^{-2} day^{-1}, but with minimal variations (Figure 4-6). Highly significant differences ($P < 0.01$) in release rates for Experiment 2 occurred due to time effects, while treatment effects were just significant ($P < 0.05$), with higher mean rates occurring in the nonaerated trials with hyacinth. Interactive effects between time and treatment were, however, not significant ($P > 0.01$) (Table 4-1).

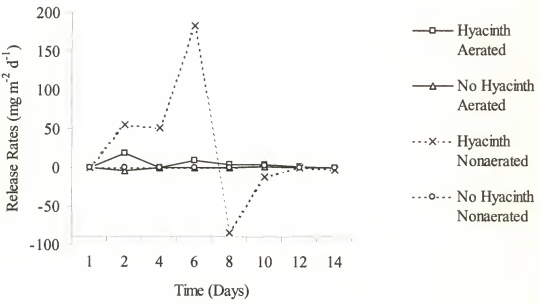


Figure 4-6. Phosphorus release rates from decomposing hyacinths, Experiment 3

Effects of decomposition and its products on water quality were reflected in depressed dissolved oxygen, low pH and high conductivity in the nonaerated setups, and an increase in water column SRP in both setups.

Discussion

Role of Decomposition of Macrophytes in Aquatic Ecosystems

Decomposition of aquatic plants in general and water hyacinth in particular, is essential for recycling organic and inorganic components in aquatic ecosystems and is influenced by several environmental and plant-related factors. These include C:N ratios of the plant, presence of organic complexes resistant to decomposition such as a waxy or cutin layer (Battle and Mihuc 2000), and dissolved oxygen in the water. Acharya (1935) reaffirmed that nutrient release from decomposing plant organic matter is controlled by the level of dissolved oxygen in the aquatic environment. Most plant tissue eventually enters the detritus pool, and microbes (both bacteria and fungi) become involved in the mineralization processes. Suberkropp (1997) considered tropical aquatic ecosystems detritus-based with decaying plant matter acting as an important energy source.

Influence of Decomposition on Water Quality

During decomposition of water hyacinth and other macrophytes, nutrients and other chemical constituents are released into the water with both direct and indirect effects on water quality and other ecosystem components. In the current study, decomposition resulted in a significant decrease in dissolved oxygen over time, leading to hypoxic or anoxic conditions. A decrease in pH that resulted in acidic conditions, with an increase in conductivity was, however, unexpected although this may occur in natural waters with poor buffering capacity, high concentrations of salts, high inorganic loading or heavy metal contamination. In some Gulf Coastal lowland lakes of Florida that have connection with underground water, for example, Canfield (1981) reported acid conditions with high conductance at 25 °C e.g., Oyster Lake (pH = 6.5; specific conductance = 4,300 mho

cm^{-1}), Western Lake (pH = 6.6; specific conductance 5,600 mho cm^{-1}), and Lake Tarpon (pH = 6.0; specific conductance = 4,250 mho cm^{-1}). In related studies on Lake Bosumtwi, Ghana, (Jannasch 1975) and Lakes Nyos and Monoun, Cameroon (Kusakabe et al. 2000), it was noted that decomposition of organic matter raises partial pressure of CO_2, thereby lowering pH, accompanied by accumulation of mineral salts that lead to increased conductivity. Thus, decomposition alters the physicochemical water environment by lowering dissolved oxygen and pH, and raising conductivity of the overlying water. Low pH due to high CO_2 partial pressure and high conductivity due to presence of salts (e.g., NaCl.) were also reported by Lahav et al. (2001) when investigating pH, alkalinity and acidity in ultrasoft waters. Studies on Imcheon Au-Ag mine in Korea (e.g., Jung, 2001) also reported high conductivity (3,820 $\mu S\ cm^{-1}$) and low pH (2.2) due to heavy metal contamination. Soucek et al. (2000) also associated low pH and elevated conductivity of an acid mine drainage of Puckett's Creek watershed in southwestern Virginia, USA, with high concentrations of heavy metals in the water column. Other studies (e.g., Franke and Franke 1999; Lopez-Archilla and Amils 1999) have reaffirmed the strong relationship among pH, conductivity and heavy metals (or persistent chemicals), resulting in low pH and elevated conductivity in soil and water. Manyala et al. (1996) also reported low pH and high conductivity in areas of industrial discharges in the Kenyan part of Lake Victoria, East Africa. Further, Singh and Jha (2000) associated low pH (5.6 to 6.7) and high conductivity (340 to 530 μScm^{-1}) in sediments of Kawar Lake (North Bihar, India) with eutrophication.

Depending on the amount of biomass undergoing decomposition, hydrological conditions, and lake morphometry, decomposition of aquatic macrophytes can have

important effects on an aquatic ecosystem. Consequences of these passed unrecorded in Lake Victoria when massive water hyacinth biomass sank in late 1998. Coupled with the increasing anoxic hypolimnion of Lake Victoria (Mugidde 1993), sinking and subsequent decomposition of water hyacinth may have aggravated the problem of anoxia and internal nutrient loading, especially in deeper portions of the lake where a persistent anoxic hypolimnion enhances P release, or in sheltered shallow bays where turnover rates of biotic and abiotic components are high. In the laboratory experiments, it is probable that low dissolved oxygen in the nonaerated trials limited formation of chemically bound P with oxidized cation species (Fe, Ca and Al); this may have accounted for significantly higher concentrations of SRP in nonaerated trials with hyacinth than aerated ones. The Kagera River continuously transports huge chunks of water hyacinth mats, most of which are fragmented by strong waves and sink to the sediment surface and may have negative effects on the water quality of nearby bays.

The effects on water quality due to decomposition associated with the massive collapse of water hyacinth that occurred in Lake Victoria are not known. However, it can be inferred, based on laboratory studies during the current study, that high nutrient loading from decaying hyacinths, depressed dissolved oxygen and pH and elevated conductivity may have altered the ecosystem including bacterial productivity (Murray and Hodson 1986). The almost continuous algal blooms in most bays could be a result of enhanced algal production due to nutrients released from the sunken water hyacinth.

Release of soluble P was significantly higher under nonaerated than aerated conditions and was highest during the first 4 to 6 days. Decomposition experiments have demonstrated that nonmicrobial processes (physical leaching) dominate the first 4 days of

decay; thereafter, the contribution of microbial processes increases exponentially and those of nonmicrobial processes decline exponentially at fairly similar rates (Gaur et at. 1992; Singhal et al. 1992; Singhal et al. 1993; Gupta et al. 1996).

Findings from the current study are in conformity with previous studies that indicated significantly higher release rates during the first 4 to 6 days (Ogwada et al. 1984; Sharma and Goel 1986). In addition, Singhal et al. (1993) and Gupta et al. (1996) indicated that most physical leaching occurs within the first 4 hours. Unfortunately my study did not take data at hourly intervals to reveal this trend.

Under field conditions, the amount of P released into the water from decomposing macrophytes may be masked by dilution effects from the large volume of lake water. Thus, highest P release rate recorded during the current study (662.82 ± 91.94 mg m^{-2} day^{-1}) may not be representative of the natural situation since the volume of water in the incubation tubes was limited (1.6 L) compared to the lake, where free exchange of water ultimately leads to dilution through various transport mechanisms (e.g., bioturbation, water currents, and diffusion). For example, Reddy and DeBusk (1991) measured decomposition rates of water hyacinth under field conditions in Lake Apopka, Florida and found P release rates of 4.4 to 5.2 mg m^{-2} day^{-1}.

Other factors may influence the amount of P released from decaying water hyacinth under natural conditions. Many plants translocate nutrients from dying plant parts to actively growing shoots (Larcher 1980). During the growing season, which is likely throughout the year in the tropics, plants accumulate major nutrients (N, P, K, etc.) for later use. With increasing age, the more labile elements (N, P and K) become concentrated in young leaves, their concentrations declining as the leaves mature and age

(Larcher 1980). Thus, by the time senescing and dead plant parts start decomposing and releasing nutrients, most of the essential elements will have been translocated to other parts, thereby lowering the amounts released into the water. In addition, senescing and dead leaves of water hyacinth may remain on the parent plant until an advanced stage of decomposition before they are shed. In this way, the plant has ample time to translocate most nutrients to active growing parts (Center and Van 1989). During this study, whole plants were harvested, moribund parts detached and the rest chopped to pieces for use in the experiments. It was inferred, therefore, that most nutrients in the dying parts had already been translocated to growing parts. It was assumed also that nutrients lost through the detached parts formed an insignificant nutrient pool in the plant tissues.

Phosphorus Release Over Time

The profound decline in SRP concentration and P release rate after the high P release rates during the initial 4 to 6 days, may be due to P assimilation by microbes, leading to formation of particulate organic P (POP). Increased SRP towards the end of Experiment 2 was likely a result of death, decomposition and subsequent release of P from dying and dead microbes. For example, Reddy and DeBusk (1991) noted an acute reduction in the C:P ratio as a result of microbial retention of P from decomposing macrophytes.

Ayyappan et al. (1988) noted an increase in total nitrogen content of water with decomposing hyacinth, indicating a compensatory nutrient influx during the process of decomposition. They found that high nutrient levels in the water due to release from decomposing hyacinth resulted in high bacterial activity. Most anaerobes are facultative and can easily out-compete aerobes under anaerobic or hypoxic conditions (Gaur et al.

1992). Oxygen-stressed waters may eliminate aerobic decomposers, leaving facultative anaerobes that enhance release of nutrients from decaying hyacinth. Products of macrophyte decomposition not only alter water quality but also may directly or indirectly alter food chain dynamics. For example, Murray and Hodson (1986) found that soluble compounds derived from macrophyte decomposition influence both bacterial secondary productivity and availability of microbial biomass to microconsumers.

Conclusions

Decomposition of water hyacinth releases nutrients, notably P, into the aquatic environment. Release is highest during the first 4 to 6 days but later declines to minimal levels. Nutrient release is enhanced under anoxic or hypoxic conditions. Under natural conditions, the concentration of nutrients released from decomposition of plant organic matter may be modified by dilution, especially in large water bodies. In small water bodies or sheltered shallow bays such as Thruston and Waiya of Lake Victoria, the problem may build to levels of concern for deterioration in water quality. The persistent algal blooms in most bays of Lake Victoria could partly be attributed to effects of nutrients released when water hyacinth sank in late 1998. The Kagera River continuously transports chunks of water hyacinth mats to Lake Victoria where they are destroyed by strong waves, sink to the lake bottom, decompose and release nutrients and organic constituents into the water. Effects of these on water quality need to be addressed.

CHAPTER 5
SUMMARY AND CONCLUSIONS

Summary

In 1988, water hyacinth was reported for the first time on Lake Victoria. It spread rapidly and in less than 10 years, most sheltered bays and most of the lake's coast was infested with the plant. Extensive mats of water hyacinth characterized most sheltered bays in the Ugandan portion of the lake, and reports from the Kenya and Tanzania sections of the lake indicated similar occurrence. Two forms of infestation were realized i.e. stationary fringing mats that varied in length and width along the coast, and variable sizes of mobile mats that drifted in the open waters under the influence of winds, waves and water currents.

The variety of names given to the plant by local people was testimony that the plant was an exotic invasive whose source was not known by them, although the native home range is Amazonia in Latin America. Rapid proliferation of water hyacinth resulted in several direct negative socio-economic and environmental consequences to the local people. Negative socio-economic attributes included, but are not limited to, disruption of fishing activities by physically covering fishing grounds, entanglement and destruction of fishing gear especially gill nets, impairment of activities at various economic installations such as water abstraction points and hydropower generation facilities. Water hyacinth also fouled docking facilities for ferry terminals at many ports on the lake. Littoral zones, especially in sheltered bays, are important breeding, nursery and feeding grounds for

many fish species, and were likewise fouled by the physical presence of water hyacinth. Due to its high biomass and productivity, sediment characteristics could have been altered in infested habitats as a result of organic matter deposition. Efforts were put in place to control the plant through mechanical harvesting at strategic sites, manual removal at fish landing sites, and use of biological control on a large scale. Among management options implemented, environmental aspects, notably nutrients, accounting for rapid proliferation were ignored. With nutrients and an absence of natural enemies, the Lake Victoria environment enhanced rapid proliferation of water hyacinth. This study tried to bridge this gap so that control options can integrate aspects of nutrients as important environmental variables influencing proliferation not only of water hyacinth, but also of other aquatic macrophytes.

The rapid proliferation of water hyacinth on Lake Victoria was a biological expression of a conducive environment for its growth. Water quality data, notably nutrients (N and P) correlated significantly with the growth characteristics. Although water hyacinth flourished luxuriantly in many bays, zones of major concern were point sources of nutrients. These hot spots, characterized by high nutrient loading, included, in order of decreasing importance, Murchison Bay, Bunjako Bay, Napoleon Gulf and the riverine ecosystems including the Kagera River. Although ambient nutrient levels, especially P, were low in most riverine systems, growth was luxuriant in such ecosystems probably due to failure of establishment of biological control, in addition to landscapes erosion that is a source of nutrients for aquatic plant growth.

The major input of nutrients to Murchison Bay is via the Nakivubo Channel that drains the densely populated urban areas of Kampala. Bunjako Bay receives most of its P

load through the Katonga River that drains cattle grazing areas within the catchment. Fielding Bay on the other hand, has a variety of nutrient sources, with major ones being sewage effluents via Kirinya stream and through Budumbuli Stream that drains upland areas northeast of Jinja. Diffuse nutrient sources are increasingly becoming important as noted from high P levels at sites near Kakira sugar cane plantation in Fielding Bay.

During growth, water hyacinth luxuriantly absorbs and assimilates nutrients from the immediate water environment. Upon senescence, death, and subsequent decomposition, assimilated nutrients are released back into the environment in proportions influenced by several environmental factors especially dissolved oxygen.

The extensive collapse and sinking of water hyacinth that occurred in late 1998 is therefore to be treated as a matter of concern, since the quality of the affected water environment was altered as water hyacinth decomposed. During the current study, laboratory-based decomposition experiments of water hyacinth resulted in depressed dissolved oxygen, acidic conditions, elevated conductivity and increased concentrations of N and P. Thus, products of decomposition alter water quality by lowering dissolved oxygen and producing acidic conditions, in addition to increasing electrical conductance. No significant differences were however, noted in carbon content of surface sediments in Thruston and Fielding bays, probably indicating no significant effects of the collapsed plant mass that occurred in Thruston Bay in late 1998. In addition, the significantly higher P released from sediments of Thruston than Fielding could be due to high P concentration that was sequestered in the plant biomass before its deposition at the sediment surface.

Conclusions

Nutrients, notably nitrogen (N) and phosphorus (P) in their available forms are among the most critical environmental factors that influence growth characteristics of water hyacinth in Lake Victoria. This conclusion supported the test hypothesis that spatial and temporal variability in ambient nutrients (N and P) influence water hyacinth growth characteristics. Plants in nutrient-rich waters (> 40 $\mu g\ L^{-1}$ SRP) exhibited luxuriant growth and high nutrient accumulation. Plants were characterized by longest and broadest leaf blades with nonbulbous (uninflated) petioles inside mats but a fringe of plants with bulbous (inflated) petioles. Plants were also greener with shorter and fewer roots (root:shoot ratios usually < 0.5). On the other hand, plants in nutrient-poor waters were characterized by shorter and narrower leaf blades, bulbous (inflated) pale-brown petioles, and with either longer (> 40 cm) or short (< 10 cm) but dense roots (root:shoot ratio approached 1 and at times > 1).

If water hyacinth infestation occurs in an aquatic ecosystem with phytoplankton as the dominant primary producers, there is expected to be alteration in the amount of organic carbon that sediment to the lake bottom. Water hyacinth-derived organic matter has more structural carbon compared to phytoplankton. This results in spatial and temporal accumulation of more carbon in surface sediments in infested bays. Effects of this on biota, was however, not known.

Decomposition of water hyacinth-derived organic matter releases nutrients especially phosphorus, with attendant alteration of water quality such as depressed dissolved oxygen conditions, creation of acidic conditions and elevation of electrical conductivity. Consequences of these on aquatic biota have not been addressed. In view of

huge amounts of water hyacinth that are transported downstream to Lake Victoria via the Kagera River, most of which are destroyed by strong waves and sink to the lake bottom, there is concern for effects of their decomposition on water quality. Further, failure of establishment of biological control in rivers, leading to persistently uncontrolled hyacinth infestations, has not been addressed.

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Wanda Fred Masifwa was born on 19th December 1963 to Mzee Yusito Masifwa and Mrs Pulusuka Muyama, Busiu subcounty, Mbale district in eastern Uganda. He had his primary school education from Busiu Primary School (1972 to 1978) in Mbale district. He joined Kiira College Butiki in Jinja district for his secondary school education (1979 to 1982); and Nabumali High School in Mbale district for his high school education (1983 to 85). He joined Makerere University, Kampala (1985 to 1988), where he pursued a B.Sc. Degree (Botany/Zoology), majoring in Freshwater Phycology and Hydrobiology. In 1991, he joined the then Uganda Freshwater Fisheries Research Organization (UFFRO) as a research assistant in the field of limnology. He undertook various courses including

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After finishing his Master of Science degree, he worked as a Research Officer at the Fisheries Resources Research Institute (FIRRI) of the National Agricultural Research Organization (NARO). Fred received his Ph.D. in Systems Ecology and Ecological Engineering, Department of Environmental Engineering Sciences, University of Florida, U.S.A. in August 2003. Fred is married to Sarah; and they have three kids (Kenneth, Fiona, and Santa).

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas L. Crisman, Chair
Professor of Environmental Engineering Sciences

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